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REVIEWS OF *BIOLOGY AND FREEDOM, AN ESSAY ON THE IMPLICATIONS OF HUMAN ETHOLOGY* BY S. A. BARNETT

Biology and Freedom, an Essay on the Implications of Human Ethology, by S. A. Barnett. Cambridge University Press, Cambridge, U.K., 1988, XVII + 376 p., \$39.50.

Biology and Freedom is a sensitive, compassionate and humane book. It is also a somewhat disappointing work. The source of disappointment is not imprecision or pretentiousness, as is so often the case when giants of science, such as S.A. Barnett, are indulging the urge to ruminate about the philosophical significance of their discipline. Rather, I find the book disappoints because it strains too hard to defeat an enemy, what I will term 'pop' biology, which has already been soundly thrashed by other worthy critical opponents in recent years. More seriously, Barnett fails to deliver on his promise to deliver "... a commonsense alternative" (p. 227) to the pop biology he is quite successful in skewering.

Barnett's goal is to persuade us that there is no threat to human freedom posed by the findings of twentieth century evolutionary biologists, ethologists, anthropologists or geneticists. He wants us to be very wary of attempts to draw lessons about the limits of human behavior based upon either the study of or speculation about other species. This thesis constitutes the bulk of the book and the author prosecutes the case skillfully and thoroughly.

Barnett goes full bore at those of his peers who study the behavior of ants, bees, rats or primates, as well as those who popularize their work in magazine articles, plays and movies, or who rush into print books bursting with all lessons drawn from the lives, loves and feuds of animals. 'Pop' biology sees the animal world as a kind of natural *Guide to the Perplexed*. If we want to know what we can be, what we should be, pop biology maintains we need look no farther than the closest hive, nest or troop.

Barnett will have none of the sloppy analogizing, definitional vagueness, and unfounded logical inference that characterizes the canon of pop biology—Lorenz, Ardrey, Eibl-Eibesfeldt, Dawkins, Wilson, and Trivers. Barnett insists that a careful review of what ethology, sociobiology and evolutionary theory have found concerning

animal behavior reveals that the only lessons to be learned are that animal behavior is complex as well as varied and, that speculations about human nature based on animal behavior rest on metaphors that owe far more to the biases, hopes and fantasies of the humans drawing the lessons than anything animals actually reveal to us.

So what could possibly be bad about a book that reminds us to be humble in the face of nature? Why grumble about a book that signals appropriate caution and skepticism in the face of the vehement, self-assured proclamations in a flotilla of paperback books, with eye-catching titles and authors to match, who are more than willing to dis-course ad nauseum on the rotten nature of human nature to any t.v. or radio talk show host within earshot?

Well, the moon of biological determinism seems to be waning these days. Many competent scholars have launched sustained attacks on crude biological determinism and pop biology during the past decade (i.e., S. Gould, R. Lewontin, P. Kitcher, among others) and they seem to have made headway against the most egregious excesses of pop biology. This is not to say that the Dracula of crude biologism does not need the occasional stake pounded into it to keep the monster dead, but it does mean that some of what Barnett has to say about the limits of metaphor, analogy and comparison has been said elsewhere by others with equal conviction and grace.

More serious is Barnett's failure to deliver on his promise of an alternative outlook to that made familiar by pop biologists. Barnett does a wonderful job of telling us what not to expect from the study of animal behavior. But his effort to construct an alternative, by warning against crude reductionism and mechanistic determinism, and by noting the power of communication, teaching and tradition as non-Darwinian mechanisms of human sociality, does not amount to enough.

The versions of reductionism and determinism Barnett targets are so simple-minded that to describe them as strawmen seems kind. When, for example, Professor Barnett warns us that "[t]he notion that everything that can be usefully said can be said in terms of physics is indeed incoherent. . ." (p. 238) he is undoubtedly right but almost no one believes this version of reductionism. The physicists most likely to espouse this sort of metaphysics found out long ago that it was false when they traded in their union cards in the 1940s and 50s and became frustrated molecular biologists.

The more interesting claim espoused by modern reductionists is that laws at higher levels of phenomena ought be consistent with, if not derivable from, those governing lower levels. Critics, ranging from devotees of punctuated equilibria theory to cladists, doubt that this sort of reductionism makes any sense since they think it rests on

a false notion of the concept of a 'level'. Yet, Barnett does not give us any advice about how he thinks we ought resolve this ongoing debate.

Similarly, when Professor Barnett is advancing his positive contribution against simple-minded pop biology he notes that, "we are accustomed to analogies between the transmission of genes and the transmission of customs . . . but the analogies are misleading" (p. 282). Again, he is surely right but he has not gone far enough. What will put pop biologists back on their heels is a non-Darwinian theory of cultural evolution. Sociobiologists such as Dawkins, Wilson and Alexander are quite willing to acknowledge the existence of culture. They simply believe it is on a short leash relative to genetics. Barnett does not tell us enough about the details of how culture and tradition are transmitted to knock this aspect of pop biology out of the ring

I have one other, smaller bone to pick with the author. In a chapter entitled "Darwinism, genetics and politics" (chapter 9, pp. 141-171), Barnett is concerned to show the horrible results pop biology can have when it is taken seriously by politicians. The chapter describes the rise of eugenics in America and England prior to the War, eugenics in Germany, and the post-War manifestations of eugenics in America and Britain in the form of debates about IQ testing and the sexism of sociobiology.

The whole chapter is thirty pages. Only 4 of these, counting generously, are devoted to the rise and flourishing of eugenics in Germany. The Soviet Union's tragic experience with Lysenkoism receives no attention whatsoever. The author seems to me to have, uncharacteristically, lost his perspective in this chapter. The fact that race hygiene theory led to mass murder in a totalitarian state should be the centerpiece of any discussion of the dangers and abuses of biologism and pop biology.

I think *Biology and Freedom* is worth reading. But it is valuable more for its boldly critical stance of sloppy thinking among those who study animal behavior than for any positive theory of how human freedom coexists with both biology and culture. But, successfully taking on a century's worth of misguided and deceiving metaphors and images can hardly be all bad!

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* * *

Biology and Human Freedom presents the reflections of a distinguished and broadly educated zoologist on the meaning of our biolog-

ical knowledge for our understanding and conduct of human life. Its principal aims are to challenge the reductionistic efforts of Darwinists and behaviorists, so prominent in this century, on scientific, philosophical, and political grounds, and to articulate a more "authentic" image of human nature, one which sanctions a political agenda more congenial to the author's democratic socialism. As such, this book belongs to the genre of works known as "Reform Darwinism," so admirably analyzed by Robert Bannister (1979), whose work is cited, but apparently not fully assimilated by Barnett. Like earlier Reform Darwinist tracts, such as Richard Hofstadter's classic *Social Darwinism in American Thought* (1955), its principal defect is its caricatured view of its opponents (ethologists, sociobiologists, behaviorists, etc.) as political thugs and moral monsters, whose works have been used to protect the rights of "the powerful, violent and selfish to kill, to coerce, to deceive or to rob others" (p. 301). Despite this defect, Barnett has succeeded in presenting an engaging and fascinating account of the myriad ways in which human abilities and practices diverge so profoundly from simplistic animal or machine analogies, while also reminding us of the real evils that such analogies have, and may still, appear to sanction.

The core of this essay is a critical examination of four powerful images of human nature put forth by some of the most prominent scientific portraitists of this century: "*Homo pugnax*" (the violently aggressive species), associated with Konrad Lorenz and his epigone; "*Homo egoisticus*" (the selfish, calculating species), attributed to social Darwinists, eugenicists, and sociobiologists; "*Homo pavlovi*" (the conditioned species), named after its creator; and "*Homo operans*" (the greedy species), as painted by B.F. Skinner and his school. For Barnett, however useful such analogies and models may be scientifically, as heuristic devices, they become both scientifically debilitating and politically harmful when raised to the level of objective truths, to be asserted uncritically rather than investigated systematically. By demonstrating how both animal and, more dramatically, human behavior diverge from simplistic models, and by reminding us of the metaphysical assumptions (primarily reductionism and determinism) upon which these models are based, Barnett reveals them to be "myths," not hypotheses: seductive images of our origins and ends designed to guide the conduct of our lives. But if they are myths, why have they been put forward so vigorously and accepted so broadly? For Barnett, the answer is simple. Such reductionist myths as the "naked ape," "man, the machine," and the "selfish gene" have served, intentionally or unintentionally, conservative, even reactionary, political functions. At best, they undermine our resolve to attack contemporary human problems and to do so humanely, while also destroying our hopes for human progress and greater human freedom.

At worst, they seem to legitimize "greed," "inhumanity" and a "lust for power" (xiv) by presenting them as fixed and permanent features of our nature.

Certainly the legacy of racism, genocide, forced sterilization, and psychosurgery which Barnett recounts is a painful reminder of the evils committed in the name of biological science. Nevertheless, there are two significant shortcomings in Barnett's presentation which, I fear, will weaken the impact of this admirable and passionately argued book. First, although the author rightly criticizes the "simplified accounts" of human action (p. 207) offered by some biologists and their popularizers, at times it is Barnett's account which unfairly simplifies their views. What ethologist speaks of a fixed, "unchangeable" human nature (p. 115), genetically controlled, which consists of "ungovernable" impulses (pp. 74, 283) expressed in uniform ways? What sociobiologist ignores the range and diversity of human behavioral and social patterns corresponding to the range of environments in which we live? What biologist would disagree that "each developmental change is influenced by the interaction of genes and environment"? Who but Barnett's own straw man believes that natural selection has "produced a species . . . with a uniform set of characteristics that fits it for a single mode of living?" (p. 115), or that "sex roles and reproductive practices are fixed and unaltered in any environment" (pp. 133, 166)? The attempts of sociobiologists and ethologists to account for human cultural diversity may indeed be ultimately inadequate, but they must at least be acknowledged.

Second, Barnett's intellectual history and sociological interpretation of such appeals to the biology of human nature does not adequately fit the facts, even as he presents them. The use of animal analogies, biological theories, and "scientifically"-based programs for social change like eugenics are not the monopoly of conservative apologists of the status quo (pp. 79, 141, 291). Barnett even acknowledges the appeals to Darwinian theory by socialists and communists and their support of eugenics (pp. 25-6, 144), yet insists on treating these abuses, including racism and sexism, as diseases unique to white, male capitalists. That appeals to "spurious biology" are the "last resort" of those who support social changes and not just those who oppose them (p. 291), that sociobiologists, in particular, are often radically opposed to the existing social and moral order (Kaye, 1986) is completely overlooked, yet amply demonstrated by Barnett's own use of the "relevant biology."

These interpretive flaws notwithstanding, *Biology and Human Freedom* remains an excellent critical survey of the modern battle over the biology of human nature, which students and laymen will find both accessible and fascinating. For professionals, its encouragement of greater care in the use of animal analogies, its call for

greater philosophical self-awareness, its reassertion of Karl Popper's distinction between reductionism as a research strategy and reductionism as a world view (p. 238), and its reminder that our conceptual language may profoundly affect our attitudes and conduct toward our fellow human beings, are vital truths which must not be ignored.

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* * *

This elegantly produced and literate volume deserves a wide audience, for it focuses attention on important scientific and social issues. Nonetheless, as an original contribution to the study of "human nature," it is a shallow piece of work, inferior in all respects (except for style!) to similar works, such as *Not In Our Genes* (Rose, Lewontin, & Kamin, 1984).

The chapters which debunk scientific myths about aggression, sociality, etc. are written in an amusing style, but rely on time-worn examples. Aren't there others? That on racial differences sidesteps the difficult but important question, what if anything is race anyhow? All in all, however, it is a pleasure to read such a well-crafted critique.

His sections on politics, economics, or culture theory, on the other hand, betray a lamentable lack of competence in the area of social criticism. Nowhere does he discuss economic determinism, nor the idea of world economic systems, nor theories of power. A work that casts as broad a net as this must be woven of finer mesh. It's not enough to mention Marx. We must also deal with Marcuse.

As to the values he champions, they are certainly attractive to most middle-class WASPS, but this denies the very diversity of values that most writers in his ideological camp would celebrate.

The obstacle to human betterment, he pronounces solemnly, is "war." This merely begs the question. Whose war? Why? If he wants us to discard biological justifications for the human condition (and we agree with him on the need for this), why does he shy

away from examining economics, market politics, power and ideology?

Science, Barnett proclaims, is a source of myths, the most powerful of which is that biology can explain and improve society. His book would be more persuasive if it merely made this point and left the moralizing and exhorting to sociologists or preachers.

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* * *

Overall, I admired this book, both in aim and execution. Directed against mis- and over-interpretation of biological findings, it ranges widely, is gracefully written, literate but not self-consciously literary, occasionally ironic, reasonable and without bombast. I enjoyed Barnett's discussions of analogy, metaphor and the implications of classification, and found his habit of articulating hidden assumptions useful. All this means that my comments are mostly about ways in which he misses maximizing his effectiveness, rather than ways in which he is misguided or wrong. I begin with the timing of the book. A discussion of the style of argumentation follows, and I conclude with an observation on Barnett's progressivism.

My first response to the book was that, however well done, it is somewhat anticlimactic. It appears several years after an outpouring of works from a similar critical perspective, many focusing on the sins of sociobiology, but others addressing Barnett's wider complaints as well: biological reductionism, conservatism or moral nihilism buttressed by evolutionary stories. Barry Schwartz (1986) even compared, as Barnett does, models of human conduct in sociobiology, behaviorism, and economics. Unfairly, perhaps, I wished for something different—a penetrating meta-analysis of the controversies, an unfamiliar slant. I say unfairly because, despite a few quite recent references, I have the impression that *Biology and Freedom* was written in roughly the same period as these others, and thus, one could argue, should not be asked to supersede them. In any case, the virtues I refer to above are enduring, and most of the book's weaknesses could have been avoided no matter when pen was put to paper; the question of timing is thus not crucial.

I do have some reservations about some of Barnett's strategies in making his case. Although he can be measured in his criti-

cism (pointing out the uses of reduction as well as its dangers, for instance) he makes rather too much use of straw persons: sociobiologists who speak only of instinctual drives and never of love or rational calculation, who ignore variability, or wish only to justify their conservatism; behaviorists who deny individual differences and describe us as treating each other like circus animals, economists who ignore nonmonetary considerations.

Effective criticism of these traditions must begin with accurate representation. I can hear the howls of protest now, and insofar as they are justified, Barnett's position is compromised, and attention is diverted from hard issues to easy ones. Some sociobiologists, precisely to counter charges of reactionary politics, have either denied the moral relevance of science or drawn liberal lessons from biology. (One can criticize these positions as well, but one must first acknowledge them.) Most make much of learning and adaptability to circumstances, and cost/benefit calculations certainly do not rule out rational deliberation. Similarly, the behaviorist's claim is not so much that we treat each other as animals rather than as persons (p. 36), but rather (as Barnett points out on p. 199) that our notions of autonomous persons are wrong. And despite the quote about economists' silence on the issue of pleasure of work (p. 215), workers' values can be factored into an economist's equations.

It seems to me that the problem is not so much that everyday constructs like love, satisfaction or duty are denied or ignored by these theorists, but that they are preempted: that they are treated as epiphenomenal, as mere means (love as a "proximate mechanism" to ensure advantageous mating) or cover stories (genetically useful self deception), or are simply engulfed by an all-encompassing definition (dignity becomes just another job incentive, while boredom is a disincentive that can be offset by better medical benefits). To counter instinct with learning, or external reward with intrinsic satisfaction, then, is not only to accept the very polarities that have sustained these acrimonious exchanges for so long, but to miss the theoretical problems posed by what I have called "black hole definitions" (1989a). Reproductive advantage, reinforcement and economic calculation can all be used to define all other categories away, so that ordinary motives and feelings, while they may be present, are subordinated to a single scheme that subverts their usual meanings. Barnett occasionally touches on these questions, but often ends up letting his points be shaped by old oppositions. This is puzzling because at other times he devotes some effort to rejecting just such oppositions.

Not only can one attack straw men, one can also *be* one. (In fact, one often leads to the other.) At times, Barnett seems to offer

himself as an easy target. He speaks of "autonomous man" long before he quotes Skinner, so at first it is easy to miss the reference. When he does discuss Skinner, however, Barnett almost seems to accept exactly what he should be challenging: Skinner's pitting of external controls against causally mysterious internal ones. To use "autonomous" in this context without clearly giving an alternative meaning is to invite confusion. In much the same way, Barnett speaks of the "validity of environmentalism," only later disavowing the position that the biologically oriented (including himself—see above comment on individual differences) have always attributed to "environmentalists": that "all are created equal" (p. 109) or can be made so. Those who hold, as Barnett does, that it is more practical to focus on changing the environment than on manipulating genes, do not usually call themselves environmentalists—any more than sociobiologists and behavior geneticists usually call themselves reductionistic biological determinists. I may be missing a rhetorical ploy here, but it seems to me that if one is trying to bring reason to an area that has been marked by exaggeration and wild shots, one should not play with loaded terms.

Traditional dichotomies reappear in the contrast between genetic and cultural transmission. As Barnett points out, traits are transmitted only by gross metaphor; they must develop by complex interactions. But neither are ideas and customs mechanically "transmitted" (Oyama, 1989b), and to attribute cultural continuity to training and imitation is to suggest mindless replication rather than the mindful construction of the world that Barnett calls for. (I did appreciate his mention of children as teachers [p. 279], and wish he had recognized that other children are not their only pupils.)

Finally, despite Barnett's disclaimers about perfectibility and progress, I occasionally found his vision of improvement a bit on the sunny side. I am not convinced that racism has steadily lost support in this century (p. 287), or that men are generally so appreciative of changes in women's status (p. 170) or that communities always benefit from the "growth of individual abilities" (p. 107)—unless those abilities are simply defined by community benefit. One could apply the sardonic point he makes on p. 130 about genetically encoded information—that anything that occurs is in some sense "encoded"—to the concept of abilities. Whatever we become, that is, we must have had the ability to become. If one keeps that point in mind, it is hard to maintain the pleasant conviction that the "growth" of abilities is necessarily a good thing. Lurking behind some of these blandly liberal statements are some largely unexamined notions of human potential and needs (p.

297). I wish Barnett had used his considerable skills in investigating them further.

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* * *

This is a textbook about human behavior that tries to avoid projecting any single, totalizing model of human nature. This Barnett achieves by using the bulk of his book for criticizing various erstwhile and currently popular perspectives, such as the Freudian, the behaviorist, the Piagetian, and, particularly, the sociobiological. His attitude seems to be that we must preserve options on human freedom, but this he tries to achieve from within a biological perspective despite his warning that we must be on guard against the "use of the prestige of science to shore up a prejudice." The level of the book is undergraduate or possibly even upper grade high school.

I was impressed by the scope of this book, and it could give undergraduates an engaging introduction to several fields at once, in particular ethology, evolutionary biology, human evolution and areas of psychology, and it has a strong, and interestingly developed, historical orientation. The book is well produced, has charming photographs (many by the author), and a useful glossary.

Barnett's book is relaxed, agreeable reading, and well-meaning. Its lack of sophistication seems good, but may be bad in an area of subtle implications. Despite failing to reference, for just a few examples, such obvious allies as the Boyd and Richerson book, Lynda Birke, Ruth Bleier, the Cavalli-Sforza and Feldman book, Mae-Wan Ho, the Levins and Lewontin book, Elaine Morgan, Susan Oyama, Henry Plotkin, Jeffrey Pollard, John Odling-Smee, T.C. Schneirla, Ardea Skybreak, Nancy Tanner, or Ethel Tobach, he does manage to construct an argument critical of sociobiology, and that seems to be the main point of the book.

Despite some good arguments, Barnett leaves out some strong ones he might have used (for example, that sociobiology, like most

science, constructs knowledge based on average properties only, and these are what his *bête noir*, "fixed human nature," amounts to), and deploys some excessively weak ones. Among these is one where he questions the validity of all behavioral homologies. In order to detoxify some rather conventional caricatures of the sociobiological position (made by them, to be sure), Barnett quite intentionally throws out the baby with the bathwater by radically emphasizing the gap between animals and humans. This he does by denying homology of human behaviors with those of other animals. This Cartesian move is a major strategy of his text, used again and again—almost a leitmotiv. Animals are said to have species-specific characteristics but humans are all variability. The resulting incoherence in a book centered around biology was perhaps an understandable result of arguing from no position within biology at all. His forthright identification of his broader political position in the last chapter and elsewhere is little help given that he does not avail himself of any biological position derived from it, which he might have constructed, for example, out of the heterogeneous authors listed above.

Other kinds of weak arguments, again rootless and frequently used, include the deconstructive elaboration of so many subclasses (e.g., human variability) within a scientifically constructed class (say, territoriality among animals) as to make that class seem meaningless, as well as the deployment of counterexamples against theories. One theory he does *not* question, however, is the Neo-Darwinian theory of evolution as applied to nonhumans.

Could natural selection work among animals without variability? Is human variability of a kind different from that upon which natural selection feeds? Are humans *not* animals? Can their behavior not be described in any general sense? These are the sorts of questions I would suppose a bright undergraduate might come to upon exposure to this book. I think these are serious questions for biology as one of society's discourses, and that there perhaps may never be final answers to some of them. Given that Darwinism is enthroned in the highest places of honor in our scientific society, one set of answers will continue to be those of the sociobiologists. It is not that sociobiologists are either stupid or particularly vicious, which, by implication, tends to emerge from this book. Their basic theory leads, by way of the field of life history studies, ineluctably to the kinds of conclusions Barnett, along with others of us, is unhappy about. Indeed, if those conclusions were somewhat different—for example, that humans are basically friendly and supportive creatures—other groups would no doubt be dissatisfied because final characterization of people is itself somehow invidious. But science leads necessarily to characterization, and Darwinian science leads to certain characteristic kinds of characterizations.

What claims to knowledge about us do sociobiologists minimally make? They claim they can construct average characteristics across cultures. This amounts to defining a "fixed human nature." In doing this they use the principle of parsimony to the effect that what is most commonly observed is most characteristic and deeply embedded. In today's jargon that becomes genetic predisposition. They claim that genetic predisposition is at least a weak force—always potential and waiting to emerge if stronger forces, including environmental ones, do not push the developing system in other directions. For an example, Barnett argues that violence is learned rather than being a genetic predisposition. But he adds (p. 71), that this is true "especially among boys." Well, that is exactly what sociobiologists would predict, and it is just the kind of prediction concerning the steady presence of weak predispositions—here, that boys are especially predisposed to "learning enmity"—they want to be able to make about people. Traits considered characteristic of a species (or race or sex or age class) are those that environmentally linked forces have not, as a rule, modulated. That does not mean that in the future they might not come under stronger or different environmental regulation. Darwinian approaches to the world, fundamentally linked to historical contingency, can *never* authentically predict what will, and only little of what will not, be the case in new environments. Furthermore, there must always be variability in characteristics that can evolve by natural selection, and so the traits of "fixed human nature," including the common predisposition of young males to violence, can be constructed only at the modes of population distribution curves—whence definable predispositions can never be more than 'common.'

Sociobiologists, like other scientists, tend not to question the historical or logical sources of their theoretical frameworks. Natural selection maximizes fitness just as competition in neoclassical economics maximizes profit. The connotations here lead any Darwinian to preferentially examine characters that could be thought of as furthering competition between like kinds. The result is a spectrum of traits, like 'aggressive,' 'nepotistic,' 'spiteful' (or their opposites, if forced to it) for *all* organisms, including plants—are people not organisms? To argue against a "fixed human nature" is to argue against applying science to humans at all. To argue against the particular components of a fixed human nature listed here is to argue against applying Darwinism to that end (Neo-Darwinism simply replaces biologically determined invidious characteristics with more precisely genetically determined ones). Sociobiologists "take primitive violence for granted" or "wish to make a case for aggressiveness as a human instinct" because that seems to be required by Darwinian theory, and, moreover, it all feels quite natural in a capitalist setting. They are not misusing their theory but simply applying it. How, in a society

such as ours, could we have avoided using science to investigate ourselves? And how, in a capitalist system, could we have avoided using Darwinian approaches in that investigation?

Richard Lewontin, in a brilliant article in the *Journal of Human Genetics*, in 1974, showed how an important scientific tool, the analysis of variance, as commonly used, could be deconstructed. His motivation was that this tool had been used by genetic determinists to construct fixed IQ differences between human races. In a subsequent television appearance he defended political motivation in science because, he claimed, all science has a political role. I believe it will eventually be necessary to subject Darwinism to an even more fundamental reexamination because what is at stake here is not a single method but an encompassing world view, one quite compatible with the subjugation of peoples and the attempt at domination of nature which fewer and fewer people are really content with.

As an example connected with Barnett's book of why a reexamination of Darwinism becomes more and more imminent, we might note that B.F. Skinner, in 1981 (*Science*, 213, 501-504) relegated his operant conditioning to a subspecies of "selection by consequences," of which natural selection is the most widely understood case. Selection is becoming a leading principle in more fields, it seems, every day ("neural Darwinism," clonal selection theory, evolutionary epistemology, etc.). Armed with a deeper critique of it, Barnett could have dealt with several of the models of man that he otherwise had to handle piecemeal. Of course, he could not really have been expected to take such a line in a textbook. Indeed, had he broached an argument against Darwinism itself, the book would very likely not have gotten published. Yet, having failed to do this, he was forced into driving the wedge of difference between humans (unselected) and other organisms (the results of natural selection). This essentially Judaeo-Christian notion is an integral part of the worldview that affords the environmental destruction that is driving more people, from their resulting discontent, to examine scientific mythologies like Darwinism more closely. What is needed today is to reinstate humans into nature in a humane fashion. In order to do that it will be necessary to tackle head-on received theories which purport to do this, but in an inhumane fashion.

So, Barnett has written an engaging but deeply incoherent book, whose title might better have been *Biology or Freedom*. I think the incoherence was forced upon him by his (probably necessary) failure to criticize Darwinism itself. After that, there may have been considerable wisdom in his decision to make the book critical of all local theories about human nature as a way of leaving open the most possibilities. Perhaps it would be a good thing to face undergraduates, so desirous of "the facts," with the possibility that there never will be

any settled facts about human nature (and eventually we might want to expand that essentially reverential stance to nature at large).

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BIOLOGY AND FREEDOM: REPLY TO REVIEWERS

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Sociobiology

Sociobiology forms only a small part of *Biology and Freedom* (B&F). I begin with it because that part has caused most excitement. Dr Salthe even regards it as "the main point of the book" though it is not.

Several reviewers make the same criticism as I now do myself: that much of the analysis of human sociobiology in chapter 8 is of declining relevance. Unfortunately, a number of recent events suggest the contrary. Here are three. (1) I have just received a paper summarising two conferences, held in 1988, on evolution and human behavior (Low & Nesse, 1989). These authors refer with approval to several sociobiological works which have been justifiably mauled by many critics, but give no hint even that they have aroused controversy. (2) Since B&F was written, new, explicitly sociobiological works have appeared which represent human beings as *forced by their evolution* to be deceivers and self deceivers. Each begins with the *deceptive* appearances (cryptic and aposematic coloring, and so on) of many animals. (For documentation and further comment on *Homo mendax*, see Barnett, 1990.) (3) The only published reviews I have seen that dismiss B&F with scorn are by social scientists whose teachings are partly based on human sociobiology. But I do not know how widespread such teaching still is or to what extent it continues to influence public attitudes. These are matters for research.

Caplan

(1) Dr Caplan complains that I fail to deliver a promised alternative to pop biology. The "commonsense alternative" to which I refer on p. 227 is to reductionism, not to pop biology. On the same page I

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say that to end B&F with a supposedly complete portrait of *Homo sapiens* would be "pretentious and shallow;" and I still think so.

(2) Dr Caplan quotes part of a sentence from p. 238. The whole sentence is as follows: "The notion that everything that can be usefully said can be said in terms of physics is indeed incoherent, because the existence of physics itself rules it out." I continue that physics is a branch of knowledge, and so "implies a knower." This is not, as Dr Caplan suggests, an attack on physicists: it is part of an examination of the various kinds of explanatory reduction. Dr Caplan also comments that "almost no one believes this version of reductionism." I wonder whether he is right. Will most readers of B&F have worked out the implications of physicalism? In 1980, sixty-one advanced students of zoology were asked to comment on this sentence: *All biological phenomena can, in the long run, be explained in terms of the physical sciences*. More than half the students (and several of their teachers) accepted this proposition as an axiom (Barnett, Brown & Caton, 1983). See also Barnett (1990) for examples of prominent scientists who sometimes seem to espouse this view or something like it.

(3) I agree that my account of the history of German eugenics could well have been lengthened to match those of Britain and the USA (*cf.* Kelly, 1981).

Kaye

(1) Dr Kaye and I agree, I believe, on all matters of substance. I am sorry that his excellent book (Kaye, 1986) reached Canberra too late for me to refer to it.

(2) But I nowhere state that racism and sexism are prerogatives of "white, male capitalists"; B&F says little on the world distribution of these "abuses;" perhaps it should have said more. But see p. 287 on racist attitudes of Chinese and black Africans. (To suggest that sexism is confined to Whites would of course be ludicrous.) Most of my criticisms concern not capitalists but the works of scholars who are unlikely to be even rich. They are, I believe, male. About their color I have never enquired. I am not much impressed by the cry that sociobiologists are "often radically opposed to the existing social and moral order;" in B&F I repeatedly and explicitly point to the evidence of the unwelcome social *influence* of their works, which is *independent of the writers' intentions*. On pp. 137-9 I enlarge on their many inconsistencies. "The neo-Darwinians just quoted have evidently not fully worked out where their arguments lead . . . [and] faced with disconcerting implications, the writers recoil" (p. 138).

(3) Where does Dr Kaye get the idea that I regard the scholars I criticise as "political thugs and moral monsters?" On p. 139 I remark

on their undoubted altruism (in the primary sense of the term). The passage he quotes from p. 301 (about "the powerful, violent and self-ish") comes from a summing up of the political obstacles to progress: it refers not to the writings of the learned but to the actions of rulers.

(4) Dr Kaye asks: "What biologist would disagree that 'each developmental change is influenced by the interaction of genes and environment'?" Probably none. Nor, perhaps, would non-biological readers of B&F. But in chapter 7 I warn the reader against accepting this truism without considering its implications, and show why I find it necessary to repeat that principle, *and enlarge on it*, over and over again. The need is exemplified by the fact that Dr Kaye complains about that sentence.

Klopfers

Economic determinism and market politics are discussed on pp. 207-12 and elsewhere. The nearest to the statement about war, attributed to me, is a sentence on p. 296: "The foremost obstacle to enlarging our freedoms is war." This is part of the discussion of obstacles to progress; it is followed by a passage on the economic and political effects of war and preparation for war. War and other kinds of violence are dealt with mainly in chapter 5. For political power, see pp. 73-6 and chapter 15.

Oyama

Differences from Dr Oyama are only of emphasis and terminology. But I do part from her on this: "it is hard to maintain the pleasant conviction that the 'growth' of abilities is necessarily a good thing." The relevant passages in B&F are on each person's need to develop skills and to perform useful and satisfying work. If Dr Oyama does not accept this principle, I wish she had used her "considerable skills" to say why!

Salthe

(1) Dr Salthe complains that I reject all behavioral homologies between human beings and animals; but he does not state what he would accept as a homolog. In several passages I not only contrast but also point to similarities between human and animal actions. See, for example, pp. 21-3 and 36 on infant behavior; pp. 37 and 251 on communication; p. 181 on conditional reflexes; pp. 190-194 on curiosity and exploration; pp. 271-3 on teaching. And on p. 117 I refer to the uses of comparing human and animal behavior. The definitive statements on homology, apparently overlooked by Dr Salthe, are on pp. 23-4 and in the glossary: in biology the term homology refers primar-

ily to *structures*. A reading of chapter 4, and of the account of exploratory behavior in chapter 10, will also show that I do not dismiss all animal behavior as species-typical and therefore invariable.

(2) Dr Salthe states that I do not question Neo-Darwinism. Modern evolutionary theory and its limitations are critically analyzed in some depth in chapter 6. If, as I might have done, I had omitted this rather knotty subject, Dr Salthe would have had valid grounds for his complaint.

(3) "Barnett argues that violence is learned rather than being a genetic predisposition. But he adds (p. 71) that this is true 'especially among boys'." The sentence from which these three words are taken is part of an account of experiments on children: "seeing violence on television increases 'aggressive' conduct, again especially among boys." The experiments do not reveal how the difference between the sexes arises. (Incidentally, I would never use the expression genetic predisposition.)

(4) Dr Salthe writes: "To argue against a 'fixed human nature' is to argue against applying science to humans at all." I do not understand either the logic of this statement or its relevance to B&F. On p. 114 I write: "It may be objected that beneath and behind human variation and adaptability, there is still a fixed human nature. Such a statement is true in the sense that the species, *Homo sapiens*, is distinct from all other species: human beings have unique features . . ." Nearly every chapter of B&F gives examples of applying science to humanity. Nor do I say that the human species is "unselected"; I assume the opposite. And particular instances of effects of natural selection on human populations are on p. 86 (sickle-cell anemia) and on p. 89 (albinism). I do, however, object to groundless Neo-Darwinian interpretations of human action and to implications of fixity which defy the facts. So, evidently, does Dr Salthe.

THE BOOK

Here are some further criticisms and comments, many of which refer to the book, not to the reviews. B&F should have been subtitled, *The Political Implications of the Human Sciences*. It is an essay in transdisciplinary study. Each section deals briefly with a vast area of knowledge. The bibliography, of only about nine hundred entries, could well—as several reviewers imply—have been much longer.

Chapter 2, on the history of misanthropy and pessimism, should have given more space to its opposite—the belief in the possibility of human improvement. Chapter 3, on metaphor and analogy, does not deal adequately with the literary uses of imagery. I wrote these introductory chapters because both topics are fundamental for understand-

ing current ideas about "human nature;" and they are not given enough attention.

Chapters 4 and 5, on *Homo pugnax*, present both the errors committed under the heading of aggression and also achievements of ethology and of the social sciences. But they do not bring out the achievements strongly enough. I have also been criticized elsewhere for not stating clearly what I think should be the role of ethology in the study of the human species. The answer is that it can provide instructive descriptions and comparisons and, sometimes, testable hypotheses; but not conclusions.

Chapter 6, on evolution, is the only one (I think) which might be much shorter. Yet the peculiarities of the theory of natural selection, and of attitudes to it, are important. This was my worst dilemma.

Parts of Chapter 7, on nature and nurture, should (I sometimes feel) be printed in letters of fire. The whole field continues to contain pitfalls which regularly trap even cautious victims. I do not know how to prevent this.

Chapter 8 presents another kind of difficulty, already mentioned. I am accused of setting up straw men—an expression I use against myself on p. 139! But the passages I quote verbatim, and the works from which I take them, are not figments of an overheated pen. (For additional examples and critique, see Kitcher, 1985, regrettably not cited in B&F.) Granted, in sociobiological works, lack of logic, inconsistencies and banality are often more prominent than tone deafness to morals. Should I therefore have further softened my criticism of the outrageous gammon published by prominent persons, and added that they are really decent chaps and didn't mean what they seem to say? I admit I am more enthusiastic about exposing error than protecting the feelings of those who commit the errors. Perhaps this is wrong. Certainly, the few people I have met who advocate or teach some form of human sociobiology are charming, virtuous and willing to indulge in amicable argument. (They are also white and male.)

I wish I had said more about the extent to which current debates in this field seem compulsively to repeat those of the past (*cf.* Crook, 1987, 1989). And if I were writing B&F now, I should be able to refer to recent works in which sociobiology is allowed to retreat—as it should—into social ethology (*e.g.*, Betzig, Borgerhoff, Molder & Turke, 1988; Porter, 1987).

Chapters 10 and 11 are on the scope and social impact of behaviorism and the alternatives to it—a subject which deserves even more attention than *Homo pugnax* or *H. egoisticus*. I should have somehow put still more emphasis here, and especially on the importance of work and play.

The remaining chapters attempt "an incomplete sketch of humanity" (p. 227). Chapter 12, on reduction and determinism, arises

from the frequent unexpounded use of these terms in discussions of *H. pugnax* and their cousins. In writing it I was led into deep waters—even into the status of psychoanalytic ideas. Should I have ventured so far? I should like to have the comments, not so much of reviewers, as of the extraordinary readers of B&F. But they would probably all differ.

Language, the main topic of chapter 13, is central to any acceptable portrait of our species. We have no authentic biological account of human speech (or of music, about which I write a little, or of mathematics, about which I write nothing). The main shortfall in this chapter concerns the kinds of sentence we utter.

A large part of chapter 14 (on teaching and tradition) presents humanity as the teaching species, *Homo docens*: a favorite topic of mine partly because—despite the vast literature on education—nobody else seems to have written much about it. (I wish somebody would follow it up.) This part should probably have been shorter. I could then have said more than I did about the findings and ideas of workers such as Cavalli-Sforza and Boyd & Richerson and about the historical aspect of tradition.

The final chapter sums up the political implications of the argument. It is too condensed for rapid reading and ought to be at least two chapters. Expansion would, of course, not make consensus more likely. Many of the problems discussed are matters of life and death. They demand unremitting debate. This justifies the kindness of the editors of IJCP in arranging diverse reviews, and of the reviewers in writing about my book and allowing me to reply.

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A CANADIAN PIONEER OF COMPARATIVE PSYCHOLOGY: T. WESLEY MILLS (1847-1915)

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ABSTRACT: A brief survey is given of the life and writings of T. Wesley Mills (1847-1915) with particular emphasis on his work on comparative psychology. He represented a position closer to Romanes than to Thorndike insofar as he felt that the intelligence of certain species of animals was often underestimated. He was also a pioneer in the keeping of diaries describing the development of sensory and cognitive abilities in the first days of life in puppies, kittens and the young of other species. He also tried to relate the development of these abilities to developments in the excitability of the cerebral cortex.

In the early days of experimental psychology, at the turn of the century, the best known Canadian writer on psychology was probably Thomas Wesley Mills, Professor of Physiology at McGill University. Although Mills was widely known among physiologists for his textbooks and various researches on the heart, the brain and the voice, he was equally well known among psychologists for his observation and theories concerning animal behaviour. In this paper, a brief account will be given of Mills' career, then a few remarks will be made on the condition of animal psychology at the time when he was most active in this area. Finally an evaluation will be made of his contributions to animal psychology. In this way we shall try to establish why Mills deserves credit both as a pioneer of Canadian psychology and as a pioneer of comparative psychology.

Mills was born in Brockville, Ontario, on February 22, 1847. He took his B.A. degree at the University of Toronto in 1871, and his M.A. in 1872. Then he went to study physiology and medicine at McGill University, where he was a colleague of the young William Osler, who went on to become one of the most famous doctors Canada has produced and who bequeathed his collection of medical books to McGill University; Osler also actively aided Mills in his subsequent career. In 1878, Mills obtained his M.D. and went to study in Europe for about 4 years, both in London and in Germany. In London he qualified for the Royal College of Physicians, and studied with Sir

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John Burdon-Sanderson. In Germany he worked with the eminent physiologist Kronecker. He also spent short periods of time with Professor Newall Martin at John Hopkins University in Baltimore. His early papers on physiology were particularly concerned with differences in the structure of the heart in various species, notably reptiles and fish, and he also worked on the cerebral cortex. In 1882, he was invited back to McGill where he successively became Demonstrator (1882-1884), Lecturer (1884-1886) and finally Professor (1886-1910) in the Physiology Department. It was while he was a Lecturer that he helped in founding an Association for the Study of Comparative Psychology in 1885; this society met regularly in Montreal and its members were mainly students and teachers of the School of Veterinary Medicine in Montreal. It seems to have provided a forum for Mills to express his views on a topic that he may have come to initially as a hobby; he kept a variety of pets himself, including dogs, and over the next 15 years or so, he wrote a sequence of articles on animal psychology which were published in the *Transactions of the Royal Society of Canada*, the *Sherbrooke Examiner* and other Canadian outlets as well as in international journals such as *Science*.

However his chief claim to fame in his own profession was his writing of outstanding textbooks such as the *Textbook of Animal Physiology* (1889). This book is noteworthy for having over 500 illustrations, and I found it unexpectedly useful, as I was skimming through it, because it contained valuable information on the "rete mirabile," that mysterious organ that Galen and the medieval scholars thought was important in the manufacturing of "animal spirits." Mills has a drawing of the rete mirabile, which is a net-like structure of blood vessels found in various places in various species and which Mills believed was important in maintaining a constant supply of arterial blood to a body region without congesting it—it is found, for example, in horses' feet. In another work written for his students, the *Outlines of Lectures on Physiology* (1886), I found Mills clarifying another part of ancient physiology for me: apparently "yellow bile," so important in Galen's theory of personality, is only found in carnivorous animals; the bile in herbivorous animals is not yellow, but green; and in humans it is yellowish-green. Another ancient humour, "black bile," probably has no referent in reality, but was guessed at by the doctors of antiquity—a full treatment of "black bile" and its variations will be found in Jackson's recent book on melancholia (Jackson, 1986). Both books clearly attest to Mills' extensive knowledge of ongoing research in physiology, including his own research on the different numbers of chambers of the heart in different species, and both books have sections that foreshadow his later writings on a branch of physiology on which he eventually became particularly expert. This was the study of voice production. All his life he

was interested in music; he contributed frequently to musical criticism and bequeathed his collection of musical literature and his violin to the McGill Conservatory of Music. His second wife, whom he married after the death of his first wife when he was 53, was an opera singer. His later books included what is apparently a classical work on *Voice Production in Singing and Speaking* (1906) notable for its excellent illustrations of the vocal apparatus. After his retirement from McGill in 1910, he spent the last years of his life active in musical circles in London, England.

Mills died of a heart ailment in 1915, and his obituary in the *Canadian Medical Association Journal* of that year was written by William Osler. Osler made it clear that Mills was not of a particularly sunny or optimistic temperament. Possibly Mills felt that his work was not properly appreciated in his lifetime, even though Osler stressed his sterling service in building up the Physiology Department at McGill. Even now Mills' work on animal psychology is little known, possibly because he did not actually work in a psychology department. In his lifetime, however, Mills' interests seem gradually to have shifted from comparative physiology to comparative psychology and Osler noted in his obituary how Mills kept private kennels and wrote two books on dogs, *How to keep a dog in the city* (1891) and *The dog in health and disease* (1892).

But the work for which he is best remembered was a compilation of his various articles on animal psychology entitled *The Nature and Development of Animal Intelligence*. The work appeared in 1898, at almost the same time as Thorndike's classic monograph on cats escaping from puzzle boxes; and indeed, Mills became intrigued with Thorndike's work and wrote a surprisingly scathing criticism of it in the *Psychological Review* for 1905. We know that Mills also corresponded with Karl Groos, the eminent German comparative physiologist, and that he engaged in a correspondence in *Science* magazine with Lloyd Morgan and James Mark Baldwin (this correspondence is reproduced in the book under discussion). In his monograph on *The Play of Animals* (English translation, 1898), Groos acknowledged that Mills was writing about young animals at the same time as Groos, and quite independently. On p. 86, Groos indirectly compared Mills' work on animals with that of Preyer on infant humans. Before describing these researches, let us briefly set the scene as it existed in comparative psychology in the 1880s and 1890s when Mills was most active. Much of what follows is based on the excellent account by Robert Boakes in his book *From Darwinism to Behaviourism* (1986).

When Darwin introduced the theory of evolution in 1859, he made it clear from the outset that instinctive behaviour in animals was itself the subject of evolutionary processes: behaviours that had been found useful in the primitive species were propagated to later

offspring. Of course, the tricky question was whether behaviour first performed by a parent could be passed on to the offspring directly in a Lamarckian fashion, or whether the mechanism of natural selection sufficed to explain the evolution of instincts as well as physical characteristics. Closely related was the issue of animal intelligence: how had intelligence evolved? Was man the end-species in the gradual evolution of intelligence? Given that animals possess intelligence of a lower order than human intelligence, what were the limits of animal intelligence? On the first issue, Lamarckianism, Darwin himself and his successor Romanes seem to have shared a propensity to believe in the inheritance of acquired characteristics and it was only at the turn of the century that the idea fell into disfavour. However, Mills wrote little on this topic and we may content ourselves by noting that in *Textbook of Animal Physiology*, Mills noted that "Instincts seem to be but crystallized habits, the inherited results of ages of functional activity in certain well-defined directions" (p. 41). On the second issue, animal intelligence, Darwin and Romanes both tended to ascribe intelligence of a fairly high order to sub-human mammals, with Romanes giving a detailed account of how dogs and apes, which he believed to possess roughly the same problem-solving abilities and memory capacities, lay only a short way below the human on the "tree" of the evolution of intelligence. But Lloyd Morgan argued for great caution in ascribing human-like qualities to animals; it was not only his canon of parsimony that made him famous, but also his belief that animals often carried out what seemed like "reasoning" or "problem-solving" on the basis of chance alone. Thorndike in 1898 pushed the pendulum even further in the direction of arguing for "animal stupidity" rather than "animal intelligence:" his cats could not apparently learn by imitation of another cat how to get out of a confining box to get food, nor could a person passively manipulate their paws to teach them the task. After Thorndike, "trial and error behaviour" became a fashionable term replacing the other anecdotal evidence favouring high intelligence on the parts of dogs and cats.

It was into this controversial milieu that Mills, with his large collection of animals, interjected a plea for caution: he tried to stop the pendulum in mid-movement and swing it back in the direction of arguing for high intelligence on the part of animals. In his 1905 paper, he gave anecdotal evidence of learning by imitation in cats and by "passive doing" in dogs, and, whereas Thorndike had claimed that a vast gulf existed between the memory abilities of animals and humans, Mills argued that the memory of a dog seemed to be surprisingly similar in nature and form to that of a human, with the difference being that humans had a "more varied fringe around that memory core" (p. 269).

In various addresses to the Association for the Study of Compara-

tive Psychology, published in his book, Mills raised a number of questions that had been discussed at the Association meetings and which warranted further enquiry. These questions included: how far can dogs be said to "understand" language? How similar is a dog's "understanding" of its own name to that of a child's? Can animals be said to possess moral characteristics? How good is the intelligence of the pig or the horse compared with that of the dog? Can animals sense the presence of water? Can sheep anticipate weather changes? How do intelligence and instinct interact in the beaver's dam-building behaviour? How do dogs and migrating birds find their way? Why are domesticated animals apparently more intelligent than their wild cousins? How do animals behave when they lose a sense, such as when they become blind? In all of these questions Mills stressed the similarities rather than the differences between animal "thought" and human "thought." He suggested that in the world of nature, the achievement of a pigeon migrating 600 miles is almost as awe-inspiring as the achievement of Mozart in writing an opera. His tendency to relate animal behaviour to human behaviour is particularly exemplified in an essay he wrote on hibernation, in which he drew parallels between hibernation in animals and unusual sleep states ("lethargy" or "stupor" states) in human patients.

Mills' objection to Thorndike's research was that by confining the cats to enclosed environments, the cat had little chance to show its intelligence; for Mills the only proper way to evaluate the abilities of an animal species was to observe it in natural surroundings all the time so that one knew exactly what experiences the animal had had; he wrote:

"Were it possible to observe an animal, say a dog, from the moment of birth onward continuously for one year, noting the precise conditions and all that happens under these conditions, the observer being unnoticed by the creature being studied, we should, I believe, be in possession of one of the most valuable contributions it is possible to make to comparative psychology". (p. 273).

In his book (p. 19), he stressed that animals' sensory abilities often exceed those of humans, and made the telling point that, just as we are often mistaken about the minds of other humans, so we are likely to be even more often mistaken in understanding the minds of animals. He also believed, on the basis of observations of squirrels, that vocal communication was more widespread in animal communities than was usually realized (p. 60) and that squirrels may be more "intelligent" than chipmunks because of their closer association with humans (p. 74).

Mills himself actually came close to fulfilling his own ideal, for he was perhaps the first to make diaries of the behaviour of young

animals from birth onwards. These diaries were reported complete in his 1898 book; he was inspired to keep these diaries by the work of Spalding (1872), who had shown that the young of certain species seem to have innate instincts for certain behaviours including food-seeking (pigs, chickens) and flying (swallows), and possibly by the diaries kept of the behaviour of human babies by Darwin (1877) and Preyer (1882). For a few years Mills kept full accounts of the psychic development of a number of species, including two diaries on litters of St. Bernard puppies, one on a litter of Bedlington terriers, one on kittens of ordinary domestic cats, one on mongrel puppies, two on rabbits, one on guinea pigs, five on individual pigeons, and several on chickens. It is impossible to summarize all this information here, but what emerges clearly from these diaries is evidence for differences between the species in the preparedness for life of the newborn: cats and dogs require weeks before they can survive on their own; whereas the other species are ready after a much shorter time to fend for themselves. To give the flavour of a typical diary, here are the first few sentences of the diary of the St. Bernard puppies:

"1st day. Almost as soon as born and freed from the investing placental parts by the dam, the puppies *cry* out, though more loudly a little later, *crawl* slowly but vigorously enough toward the teats of the dam, and at once, in most cases, begin to *suck*. It is noticed, however, that other parts are sometimes sucked as well as the teats. They huddle together, and get between the legs of the dam, and where the hair is longest, or where, for any reason, there is most warmth, when not actually nursing.

Their movements are very slow. Their eyelids are still not grown apart nor their ears grown open.

Two of them weighed at the end of about twenty-four hours 1 lb. 2 oz. and 1 lb. 6 oz. respectively.

They were not examined as to reflexes other than sucking, reaction to temperature, etc.

I made, on the first day, the following experiment: placing a puppy on a surface above the floor, it was found that, when it reached the edge it became very *uneasy*, spread its claws, etc., to avoid falling off.

On this and later dates, they cry apparently from cold or hunger or when removed from the usual environment.

4th day. The last experiment is repeated under slightly varying conditions. A tortoise placed under the conditions walked or tumbled off. On this day, one puppy was conveyed to my laboratory, wrapped up warmly in a blanket, without a cry or other sign of discomfort, the journey occupying about half an hour." (p. 118)

This extract will have given some idea of Mills' reporting strategy: he does not examine the animals all the time, but at intervals;

he reports what they can do at different ages, sometimes determining the animals' abilities by small experiments and by comparing them with other species (as with the tortoise in the quotation); and he is particularly concerned to establish what seems to be innate. In this respect he was more ready to admit of the role of learning in infantile behaviour than was Spalding. In other observations, he examined the roles of taste and smell in the puppies' behaviour, the growth of the use of the eyes and ears in the first few weeks of life, the use of vocalization (he noted that a 13-day puppy will growl in its sleep), and the onset of play, which both Mills and Groos believed to be of great importance in the animal's development. Of particular interest were Mill's observations on the age at which memory and learning first seemed to show up directly. In St. Bernard puppies, Mills believed that the puppies recognised their mother by sight alone by about the 13th day, and he recounted how he accidentally trod on a puppy on the 45th day and that the puppy later showed fear of Mills; the inhibition of behaviour following punishment can be established from about this time on. Habits peculiar to dogs can be observed at certain key ages: lapping milk, as opposed to sucking movements, occurs at 17 days; barking at 25 days; scraping at a site where it will sleep occurs at 41 days, as do the movements typically made by dogs prior to defecation.

Mills' comments on his observations are perhaps even more interesting than the dispassionate diary entries themselves. He was among the first (perhaps *the* first) to show that infant animals fear the loss of support, a point J. B. Watson would later elevate into a dictum of child psychology (Watson, 1930, p. 153). He distinguished between genuine hearing in puppies and the sensitivity of the puppies to air-concussions on the skin. He noted that play only occurred after the animal had a full repertory of senses, with ears developed and eyes opened (the later usually taking place around the 11th day). He tracked the transition of vocal sounds from kitten-like whining through growling to barking. Emotions, he suggested, developed at different rates in different breeds, terriers, for example, being relatively early to show anger. The development of "voluntary" behaviour, a subject requiring perhaps more directed research than can be obtained by irregular periods of observation, was noticeable in Mills' subjects by about the 17th day, while evidence of reasoning, memory, and imitative behaviour were apparent after about a month. In research reported later in the book, Mills tried to establish correlations between the development of "intelligent" behaviour and the excitability of the cortex to electrical stimulation. His main discovery was that animals such as guinea pigs that matured early in comparison with cats or dogs also had brains that were excitable almost from

birth: the longer it took before "intelligent" behaviour became manifest, the less excitable the cortex during the period preceding the manifestation of such behaviour.

Mills also kept an interesting diary on kittens, whose eyes open at about 8 days, earlier than in the puppy, and who could learn to use the sandbox at about 30 days. He believed that the intelligence and "character" of cats was underestimated, noting the diligent efforts on one of his kittens to get into a favorite bookshelf when blocked from doing so. He believed that kittens had an instinctive "fear or dislike of the dog" (p. 224), and were in advance of puppies in the acquisition of voluntary behaviour and perhaps in other intellectual capacities. Readers who own pets will probably enjoy Mills' summary of the differences between cats and dogs:

"The greatest difference between the cat and dog is in their relations to man and to their own species.

The dog is essentially a social and a gregarious animal; the cat an independent and solitary creature, traits which are early shown.

The dog is docile in the highest degree; the cat to a slight degree as compared with the intelligence she possesses.

The cat is far in advance of the dog in power to execute highly complex coordinated movements.

In both the dog and the cat the play instinct is early and highly developed, but in the manifestation of this, the peculiar qualities of each are well established.

In will-power and ability to maintain an independent existence, the cat is superior to the dog.

In the higher grades of intelligence, the wisest dogs are much in advance of the most knowing cats, which is foreshadowed, if not actually exemplified, in the early months of existence." (pp. 232-233).

Mills observation on other animals, including guinea pigs, rabbits, pigeons, and domestic fowl, are noteworthy because he stresses how, the more important a capability to the life of a creature, the earlier the capability develops, be it smell in dogs, touch-sensitivity in rabbits, or pecking in hens. Mills' observations on drinking in chickens were associated with the controversy with Lloyd Morgan and Baldwin, already mentioned, in the pages of *Science*: the question was whether "drinking" in birds was instinctive or learned. Mills was one of the first to establish that if a chicken's beak be put into water, it will drink, but it would seem that it will not drink *unless* there is the prior stimulus of beak-in-water. So, as Lloyd Morgan, pointed out, a chicken could *see* water but never drink any, hence the controversy over whether chickens need to "learn" to drink. This literature, reproduced at the end of Mills' book, is a clear fore-runner of the revolution in our thinking about instincts brought about by Tinbergen (1951) and others with their conception of the "innate releasing stimulus".

As hinted earlier, it is not clear just how far these pioneering diaries were known outside Canada. What is clear is that Mills knew the literature on animal psychology that was available at the time (in 1896 he gave a short address on the expansion of animal psychology in the preceding decade; this address is reproduced on pp. 46-51 of *The Nature and Development of Animal Intelligence*). He favoured both observation and experiment, rather than anecdote, as methods for studying animal intelligence, provided the experiments gave the animal a chance to demonstrate its capabilities. And he had high hopes for the future of animal psychology. He described his own position succinctly in the 1905 paper:

"[In thinking highly of animals' intelligence] I have been myself classed by one of my reviewers with Romanes. While I agree with much in Romanes' attitude in regard to animal intelligence, nevertheless, since this writer preferred to work upon second-hand material rather than make observations and experiments for himself, and had, moreover, a tendency to speculate rather than the accumulation and weighing of facts, I prefer myself to be considered a humble follower of Darwin, who, so far as he went in animal psychology, best illustrates the method and especially the spirit that will, I think, prove most fruitful". (p. 271)

This would be a fitting epitaph for a scholar whose observations on comparative psychology are as valuable now as when he made them over a hundred years ago.

ACKNOWLEDGEMENTS

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ODOUR PREFERENCES AND DISCRIMINATION IN CAPTIVE RINGTAIL POSSUMS (*PSEUDOCHEIRUS PEREGRINUS*)

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ABSTRACT: Olfactory communication has been shown to be important in marsupials and, specifically, in *Trichosurus vulpecula* and *Petaurus breviceps*. Despite its commonality, little is known about the communication in the ringtail possum, *Pseudocheirus peregrinus*. Therefore, to investigate olfactory communication in the ringtail possum, two experiments were conducted. The odour preference experiment examined the importance of fur, salivary, faecal and urinary odours in ringtail possum olfactory communication. The latency to approach urinary odours was significantly longer than for any other odours. Males sniffed familiar female urine samples for a significantly shorter duration than any other odour samples. Fur samples were manipulated for longer durations than any other odour samples. The discrimination experiment examined the ability of ringtail possums to discriminate between urine samples, and hence obtain socially significant information from such odour sources. The ringtail possums showed that they were able to discriminate between individuals and between sexes. The possible functions of urine, fur and perianal gland secretions are discussed.

Very few studies have investigated olfaction as a means of communication in marsupial species, but its importance is not disputed. Information on olfactory communication has mainly been derived from studies on social organisation and ecology of species, but two notable studies concentrating on olfaction are those of Schultze-Westrum (1965) and Biggins (1979) on *Petaurus breviceps* and *Trichosurus vulpecula*, respectively. Only the latter has the support of a detailed field study enabling the information to be related to the free-ranging animal. Consequently, our understanding of the function of odours remains superficial. For example, we still know relatively little about the motivation behind marking behaviour.

The importance of olfaction in marsupials is indicated by their possession of extremely prominent olfactory bulbs which in some instances make up almost half of the forebrain (Johnson, 1977). They also have well-developed vomeronasal organs with extensive olfactory epithelium (Negus, 1958). Marsupials possess a variety of potential

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scent glands and behaviour patterns involving these glands, such as olfactory investigation and marking behaviour (Russell, 1985). All of these features are exhibited by the various possum species, as reviewed by Biggins (1984) and Russell (1985).

The ringtail possum, *Pseudocheirus peregrinus* is common and found in close association with urbanisation, yet there is only one detailed study on its social organisation (Thomson & Owen, 1964). In this study, ringtail possums were shown to be gregarious, nocturnal, and arboreal, and to live in communal nests of mixed sexes and ages but the possums' social interactions were not described.

Tyndale-Biscoe (1973) concluded that the ringtail possum does not communicate olfactorily even though this species possesses labial glands (Biggins, 1979), and two pairs of paracloacal oil glands (Bolliger & Whitten, 1948). Saliva, faeces, and urine are also odorous substances which are readily available and are potential olfactory messages in this species. Both olfaction and auditory modes of communication are likely to be the most important in nocturnal animals but the ringtail possum appears to have a limited vocal repertoire (Biggins, 1984). Therefore, further study of the role of olfactory communication in this species is clearly warranted.

The present study investigated odour preferences and odour discrimination in ringtail possums. The odour preference experiment determined odours that are of importance in ringtail possum olfactory communication, and the behaviours that are elicited by these odours. The odour discrimination experiment examined the ringtail possum's ability to discriminate between odours of apparent social significance using an operant conditioning technique.

MATERIALS AND METHODS

Animals

Six adult hand-reared ringtail possums, (2 male and 4 female), and four adult wild caught ringtail possums (2 male, 2 female) were used as experimental subjects. *Petaurus breviceps* was used as a source of odours for comparison with those from the ringtail possum. This species was chosen because of its potential habitat overlap with ringtail possums in the wild, and because it is a member of the same family (Petauridae).

Housing and Feeding

The ringtail possums were housed in three groups of three (1 male, 2 females) in outdoor metal and timber cages (dimensions

2.1m \times 1.8m \times 1.1m), and a single male was housed in an indoor 'rabbit' cage (dimensions 0.48m \times 0.63m \times 0.8m). Black plastic was taped to the cages on the sides opposing the neighbouring cage to reduce odour transfer between the cages and so maintain three relatively separate groups. All possums were maintained on a diet of fruit, vegetables, eucalyptus leaves, native flowers and bread. The food was made available in the evening, or as appropriate for each experiment. Water was provided ad lib.

Odour Preference Experiment

Each test possum was exposed to its own urine, faeces, saliva and dorsal fur and that of familiar and unfamiliar conspecifics of both sexes. One male was not tested against familiar male odour stimuli although he was exposed to all the other odour stimuli. Faeces, saliva and dorsal fur of sugar gliders, and distilled water were used as the controls.

Urine and faeces were collected by housing the possums individually in metallic cages with wire floors and a metal tray beneath or by stimulating the possums to urinate into a large metallic funnel. Urine that was free from faecal and food contamination, and faeces free from urine contamination were collected as soon as possible after excretion. The samples were sealed in glass vials or self-sealing plastic bags and refrigerated and used that night or frozen until use. Freezing reduces the loss of volatile odours. Urine and faecal samples could not be standardised for age, or the urine for the concentration of paracloacal gland secretion (i.e., milkiness). However, the variation between samples appeared to be due to an individual rather than a methodological difference.

Saliva was obtained by wiping inside the lips and angle of the mouth with filter paper. Fur samples were collected by wiping the filter paper across the dorsal fur.

Five drops of urine were applied to the test filter papers. The faeces were rubbed across the filter paper to eliminate differences between faecal size. Five drops of distilled water were used to moisten the filter paper discs as this appeared to match the moistness of the urine samples. New vinyl gloves were used for each odour to prevent cross-contamination.

The possums were tested individually in separate rabbit cages (0.48m \times 0.63m \times 0.8m) which contained a nest box, a branch and a cardboard tray (0.03m \times 0.23m \times 0.37m).

The odours were presented to the possums on two filter paper discs (Whatman Number 1, 5.5cm diameter) which were placed 10cm away from each other on a paper towel lining the cardboard tray. The

paper towel was replaced after each trial to prevent the odours from contaminating the cardboard tray.

To minimize the effect of the experimenter on the possums' behaviour, a low-light National WVP-F10N System video camera was used. A monitor placed in another room enabled the experimenter to observe the animals' responses. Red lights were used to illuminate the test area. A light dimmer was used to reduce the light intensity to the minimum required by the camera (i.e., 7 lux).

Procedure

The possums were habituated to the rabbit cages over at least two nights prior to testing. One wild female did not adapt, reducing the sample size for this experiment to nine. The possums were then exposed to pairs of clean dry filter paper until their interest in them had waned in order to eliminate the effect of the filter papers as novel objects. Tests were run after sunset when the possums had emerged and commenced feeding. The 24 different odour stimuli were divided into four groups of six (Table 1). These were presented to the possums one at a time. Each group of six was randomised so that the order of presentation was different for each of the two repetitions. A period of 48 hours was allowed between repetitions to prevent the possum from becoming over-familiarised with the odours.

Three measures of behaviour were recorded using a Canon X-07 Handheld Computer.

1. Approach—time measured from when the head of the possum was less than 30cm from the odour sample, as estimated by the investigator, and the possum had orientated toward the sample, and was obviously approaching it.

TABLE 1
Odour Sources Used in the Odour Preference Experiment

Odour Type	Odour from:					
	<i>Own</i>	<i>Sugar glider*</i>	<i>F male</i>	<i>F female</i>	<i>UF male</i>	<i>UF female</i>
Fur	x	x	x	x	x	x
Saliva	x	x	x	x	x	x
Faeces	x	x	x	x	x	x
Urine	x		x	x	x	x
Water*						

Note. Sugar glider and water samples were used as controls. F = familiar (housed in the same cage), UF = unfamiliar (housed in different cages).

2. Sniff—time recorded when nose was less than or equal to 2cm from the odour sample.
3. Manipulation—time recorded when the possum had made contact with the odour sample with more than the nose.

Approach was not recorded if the possum was accidentally in the odour sample's proximity before focusing its attention on it. Sniffing and manipulation behaviours were always scored separately. It was assumed that the important odours were not volatile and hence required close olfactory investigation.

Odour Discrimination Experiment

The paradigm used in this experiment was based on that of the Wisconsin General Test Apparatus procedure. In this method, the reward is a direct result of the animal's behaviour, providing contiguity between response and reward, and it exploited the possum's natural tendency to manipulate food and other objects with its forepaws. The discrimination apparatus was portable and could be easily removed from the cage as required, thus enabling the investigator to replace the food reward unobtrusively. This apparatus is shown and described in Figure 1. A movable false base made of cardboard was placed in the lower can. Two filter papers (Whatman Number 1, 5.5cm diameter) were moistened with the appropriate odour and attached to the front and back of each can by adhesion of the liquid to the can surface. The cans were washed with pyroneg when the odour stimuli were changed.

To train the possums on the apparatus, food from the possum's daily ration was placed in the top halves of both sets of cans to get them used to taking food out of the cans and to promote the association between the cans and food. Once they had become accustomed to this procedure the lids were placed half on, and then completely over the cans until the possums were removing the lids to obtain their food. Discrimination learning was then commenced.

The Odour Preference Experiment had indicated that urine was a significant odour for the ringtail possum. Consequently, urine samples taken from the ringtail possums were used as the odour stimuli in the discrimination experiment. Table 2 shows the various pairings of the odours tested. The possums were trained using the odour pairing of water and their own urine. The positively reinforced odour was counterbalanced so that for one male and one female, for example, their own urine was positive, while for the other three possums water was the positive stimulus. The urine was collected and handled as for the Odour Preference Experiment.

A food reward was used to reinforce the possum's lid removing

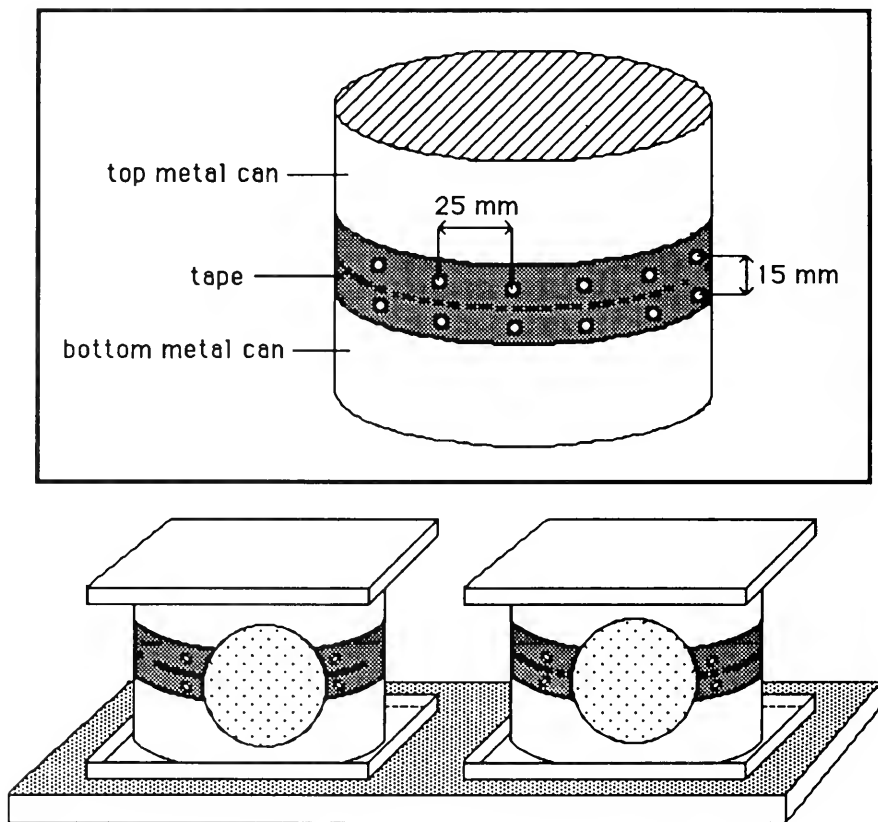


FIGURE 1. Discrimination Apparatus: the bases of two pairs of cans (height 34mm x diameter 75mm) were soldered together. Black tape covered the central join. Two rows of 1.5mm diameter holes were drilled around the circumference of both cans of each pair (inset). Metal bases (90mm x 90mm x 10mm) were attached to a board (13mm x 170mm x 350mm) 125mm apart, and each pair of cans was attached to these bases. Metal lids identical to the bases were placed on top of the cans.

behaviour in response to the positive stimulus. This food was placed on the floor of the upper can of the pair to which the positive odour was attached. The negative odour stimulus was attached to the other pair of cans. A false reward was placed immediately below the floor of the upper can of the pair and so was inaccessible to the possum. The possum's food intake prior to the trials was not reduced as they were sufficiently motivated by hunger at feeding time to perform the de-

TABLE 2
Odour Pairings Used in the Odour Discrimination Experiment

<i>Pair of Odours</i>	<i>Animals tested</i>			
	<i>Columbine</i>	<i>Mintie</i>	<i>Mars</i>	<i>Scrumpy</i>
Own vs water	x	x	x	x
Own vs UF male	x			
Own vs UF female	x	x		
F1 female vs UF1 female	x			
F2 female vs UF2 female	x			
UF1 female vs UF2 female	x	x	x	x
F1 female vs F2 female	x			
UF female vs UF male				x
F male vs UF male		x		
UF1 male vs UF2 male	x	x	x	x

Note. Only urine samples were used. F1 = familiar animal 1, F2 = familiar animal 2, UF1 = unfamiliar animal 1, UF2 = unfamiliar animal 2.

sired behaviour for a food reward. On completion of the nightly trials the possum was given its normal food ration.

Discrimination Learning

The possums were again tested individually indoors in the rabbit cages using red lights for illumination. The possum's responses were monitored from an adjacent room using the National low-light video camera.

The first possum was tested using massed trials in accordance with past investigations (Friedman & Marshall 1965; Tilley, Doolittle, & Mason, 1966; Jenkins, 1985) which suggested that learning in marsupials is enhanced by this method. However, this was found to be unnecessary and the remaining trials were in the blocked format. Depending on the possum's progress, blocks of 12, 16 or 20 trials were run with a maximum of three blocks per night. Each block of trials tested a different odour pair and there was an interval of 10 min. during which the possum was allowed to eat a native flower. The position of the positive stimulus was altered in accordance with the chance stimulus sequences for discrimination tasks devised by Fellows (1967). A correction method of training was used whereby the possum was able to correct its initial wrong choice and obtain a reward, although only the first choice was scored. The possum was considered to be discriminating when it made $\geq 10/12$, $\geq 13/16$ or \geq

16/20 correct responses on two consecutive days for a particular odour stimuli pair. The probability of results such as these occurring by chance alone is 0.019 (Binomial test, SSPS, Inc., 1986).

RESULTS

Odour Preference Experiment

The data on latency to approach, and duration of manipulating odour samples were analysed using three-way ANOVAS (SSPS, Inc., 1986). These ANOVAS looked at the effects of sex, odour type and odour familiarity on the three behaviours and showed that the type of odour affected both approach ($F(3,382) = 4.286, p = .005$) and manipulation duration (s) ($F(3,382) = 4.141, p = .007$). Examination of the means using the Student-Neuman-Keuls procedure showed that the latency to approach urine samples was significantly longer than for any other odour samples (Figure 2), while fur samples were manipulated significantly shorter than other samples (Figure 3). The manipulation behaviours which occurred included picking the odour sample up with forepaws, and/or chewing or licking the sample briefly. One extended behaviour pattern was performed by one female and two

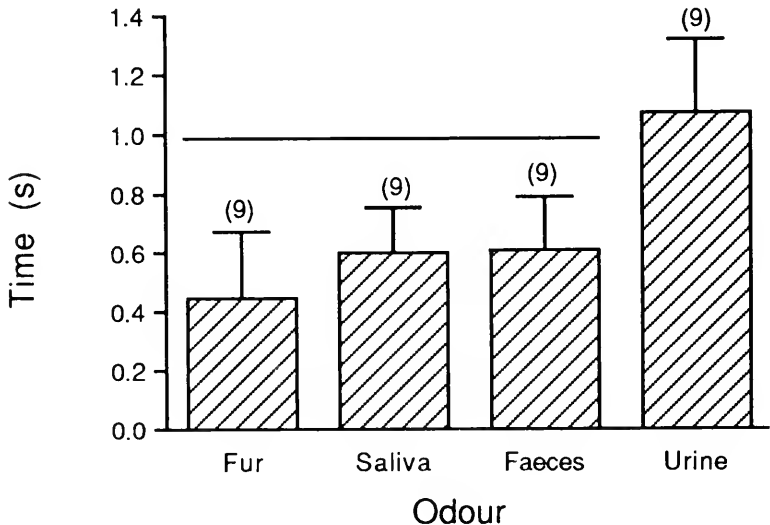


FIGURE 2. Odour Preference Experiment: comparison of the means for the latency (s) to approach odour samples depending on the odour type. The line joins odours for which the means were not significantly different (Student-Neuman-Keuls, $P > 0.05$).

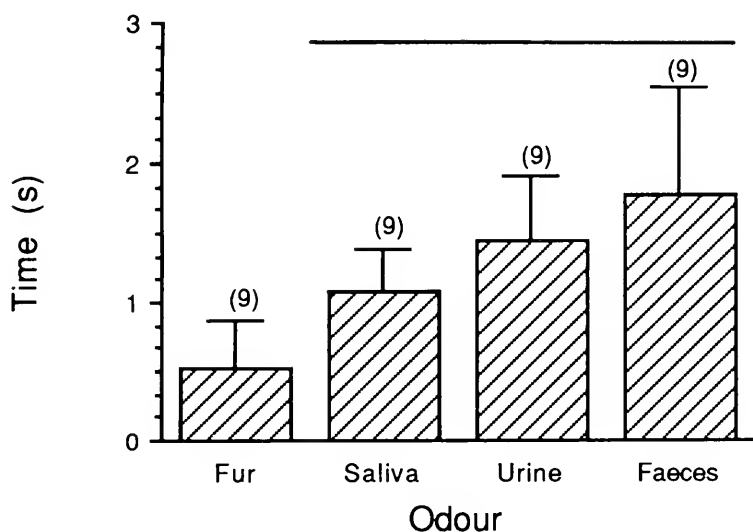


FIGURE 3. Odour Preference Experiment: comparison of means showing the effect of odour type on the duration (s) of manipulating odour samples. The line joins odour types for which the means were not significantly different (Student-Neuman-Keuls, $p > 0.05$).

male possums. Briefly, the paper was picked up with the mouth or forepaws and thrust underneath the possum's body using the hindlegs to help push it behind the possum, or into its tail.

The data on sniffing duration (s) were analysed using a two-way ANOVA which revealed a two-way interaction between sex and odour ($F(23,384) = 1.635$, $p = .034$). An examination of the means showed that there were no significant sex differences in sniffing duration. One-way ANOVAS were used to investigate the differences in sniffing separately for the two sexes and only a significant effect for males ($F(23,168) = 1.602$, $p = .048$) was revealed. However, a Student-Neuman-Keuls test failed to reveal any significant difference between means. Mann-Whitney U (two-tailed) tests examined the effect of a individual's sex on its sniffing behaviour. The only significant difference was that males ($\bar{X} = 7.000 \pm 9.502$ s; $n = 8$) (Figure 4A) sniffed familiar female urine for a longer duration than did females ($\bar{X} = 0.2 \pm 0.422$ s; $n = 10$) (Figure 4B) ($U = 13$; $P = .008$).

Odour Discrimination Experiment

Five hand-reared possums (2 males and 3 females) were trained to discriminate between pairs of odours. The results (Table 3A) show

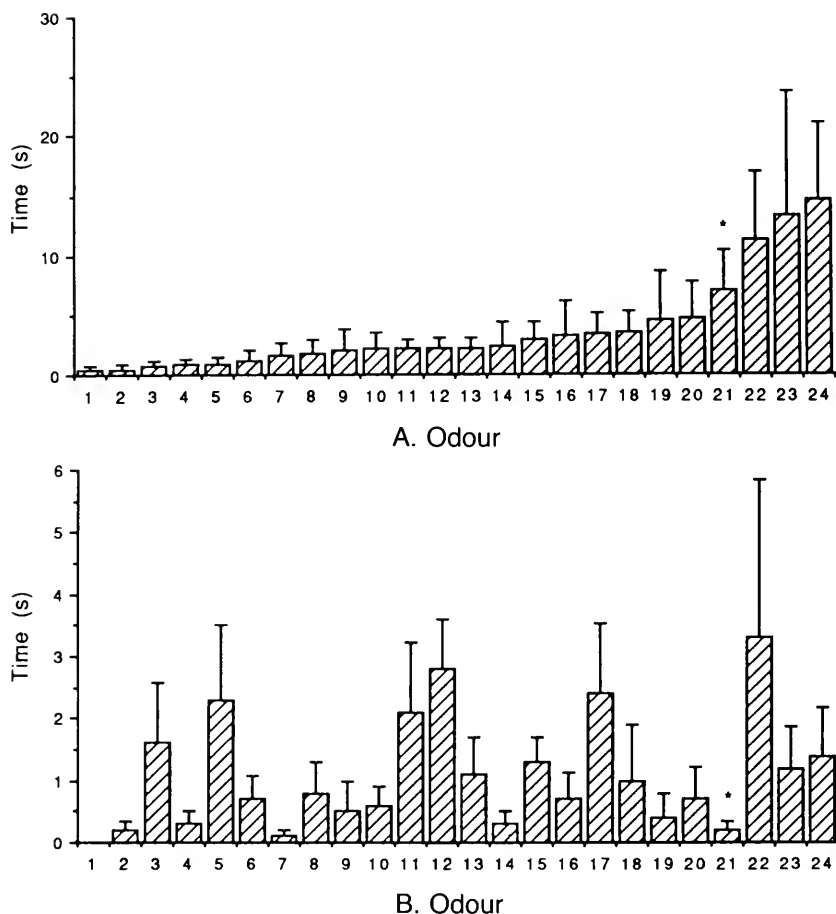


FIGURE 4. Odour Preference Experiment: Comparison of the means showing the effect of the odour sample on sniffing duration (s) ($n=7-10$) in A: males and B: females. *Indicates significant difference between sexes for sniffing duration (Mann-Whitney U (two-tailed) tests). Bars represent standard errors. Key: 1 - familiar male fur, 2 - own faeces, 3 - unfamiliar male fur, 4 - familiar female fur, 5 - familiar female saliva, 6 - sugar glider fur, 7 - own fur, 8 - familiar female faeces, 9 - unfamiliar female fur, 10 - own saliva, 11 - unfamiliar male saliva, 12 - sugar glider faeces, 13 - own urine, 14 - unfamiliar female saliva, 15 - familiar male faeces, 16 - familiar male urine, 17 - unfamiliar male faeces, 18 - water, 19 - familiar male saliva, 20 - sugar glider saliva, 21 - familiar female urine, 22 - unfamiliar female urine, 23 - unfamiliar female faeces, 24 - unfamiliar male urine.

TABLE 3A
Discrimination Test Results

<i>Discrimination</i>	<i>Possum</i>	<i>Sex</i>	<i>Trials to Criterion</i>	<i>No. of Errors</i>
<i>Own vs water</i>				
	Columbine	male	54*	16
	Mars	male	28	3
	Mintie	female	24	3
	Scrumpy	female	24	1
	Mouse	female	24	2
<i>UF1 female vs UF2 female</i>				
	Columbine	male	28	5
	Mars	male	24	2
	Mintie	female	24	1
	Scrumpy	female	36	6
	Mouse	female	24	2
<i>UF1 male vs UF2 male</i>				
	Columbine	male	24	4
	Mars	male	32	4
	Mintie	female	28	3
	Mouse	female	36	6
	Scrumpy	female	no attempts	

Note. For this test, each possum was tested. F1, F2, UF1, UF2 as for Table 2. Criterion = $\geq 10/12$, $\geq 13/16$, or $\geq 16/20$ correct on two consecutive nights.

Massed trials were used on the first night.

that they were able to discriminate between water and their own urine, between the urine of two unfamiliar females, and between the urine of two unfamiliar males, except for Scrumpy who made no attempts to discriminate between the latter odour pair. Other discrimination trials were also run for individual possums (Table 3B). Columbine discriminated between his own urine and that of an unfamiliar male and an unfamiliar female, between familiar and unfamiliar female urine, and between familiar female urine samples. Mintie discriminated between unfamiliar and familiar female urine samples, and Scrumpy discriminated between unfamiliar female and unfamiliar male urine samples.

Observations

A number of behaviours which were assumed to be involved in olfactory communication were observed during the course of this study.

TABLE 3B
Discrimination Trials Run with Individual Possums

<i>Discrimination</i>	<i>Possum</i>	<i>Sex</i>	<i>Trials to Criterion</i>	<i>No. of Errors</i>
<i>Own vs UF female</i>	Columbine	male	28	4
	Mintie	female	28	3
<i>Own vs UF male</i>	Columbine	male	24	1
<i>F female vs UF1 female</i>	Columbine	male	28	5
<i>F female vs UF2 female</i>	Columbine	male	44	7
<i>F1 female vs F2 female</i>	Columbine	male	24	3
<i>UF female vs UF male</i>	Scrumpy	female	24	0
<i>UF male vs F male</i>	Mintie	female	24	1

Note. F1, F2, UF1 and UF2 as for Table 2.

1) When the possums were extremely frightened such as when the wild animals were handled, they exuded a viscous creamy coloured secretion from their cloaca. Its suggested source is the paracloacal glands.

2) At least three variations of micturition were observed:—

i) Casual micturition appeared to be normal micturition without any special marking function (c.f. Ewer, 1968). The possum moved to a specific location and eliminated the urine where it stood without any postural changes. This behaviour was generally performed by females or subadults and occurred in the same location on the floor of the cage each night. Occasionally though, micturition was followed by a short urine dribble (or cloacal drag) where a trail of very milky urine was sometimes deposited. On drying, a white powdery mark often remained.

ii) Urine dribbling (or cloacal dragging). It was difficult to determine the difference between urine dribbling and cloacal dragging. The behaviour appeared to be a combination of the two. A distinction may be made when the quantity of urine in comparison with paracloacal gland secretion is minimal. Russell (1986) also found it difficult to differentiate between the two behaviours in *Tarsipes rostratus*.

The behaviour is an example of dispersive scent marking, although it may also have a passive marking function. Contact of the feet and other bodily areas with the substrate would result in the passive transfer of this urine to these areas. To perform this behaviour the hind-quarters were lowered with the tail at approximately a 45° angle to the substrate. The protruding cloaca touched the substrate as the possum waddled forward at various speeds along a branch or the substrate. As the possum proceeded, urine was dribbled out of the cloaca. Occasionally, faeces were also dropped along this line. These urine trails were usually a sigmoid pattern especially when they were performed on the cage floor. The urine varied in colouration from clear to milky. Viscosity also increased along this gradient and the quantity of urine eliminated varied. Males particularly, marked the same branch or same location several times in succession, and frequently throughout the night. This behaviour increased in frequency when the possums were excited, disturbed, or thwarted by the investigator, or were investigating a cage odourised by another possum. The possums were generally aroused when performing this behaviour. This behaviour was performed when the possums were placed in novel cages, such as the rabbit cages but was not performed in response to novel objects in home cages. On drying, a persistent white powdery mark usually remained. Although not quantitatively measured, the males appeared to urine dribble significantly more than the females when in their home cages. However, when isolated in the rabbit cages the females also frequently 'urine dribbled.' Urine marking, and milky urine were not observed prior to the possum's sexual maturation.

iii) Urine squirting. This micturition pattern is also an example of dispersive marking. Clear to milky urine was ejected in short frequent bursts as the possums ran erratically about the cage to escape from human contact. Occasionally they also secreted pure secretion which remained coating the cloaca.

3) On standing, a white precipitate settled out in urine samples. If the urine was shaken or aerated it changed from greenish-brown to reddish-brown. Bolliger and Whitten (1940) report the same observation in reference to *T. vulpecula*.

4) Defecation occurred frequently and at any time or place, including the nest box, and with no special associated behaviour pattern except when possums practised coprophagy. Defecation is an example of passive marking. Defecation also occurred when the possums were highly aroused such as when they were caught and restrained.

5) Sniffing rarely occurred when possums in their home cage met. However sometimes naso-nasal, naso-cloacal, and pouch sniffing, as well as sniffing the base of the tail occurred, usually initiated by

males. Males would also sniff where a female had urine dribbled, the site where a female had been sitting, and at casual micturition sites. The possums would also sniff other parts of a foreigner's body such as the feet. Naso-nasal sniffing was usually a reciprocated behaviour and would extend to sniffing the corners of the mouth and ears, although it was brief. The recipients of the other forms of sniffing usually responded aggressively by hitting out and attempting to bite.

Males became intensely interested in females at certain times of the year (presumably during oestrus) and correspondingly the frequency of their sniffing increased. Sniffing frequency was also high when the possums met a foreigner or 'familiar' individuals from which they had been isolated for several days. Female-female interactions involved naso-nasal sniffing while male-female interactions involved sniffing of the female's cloaca and sometimes the pouch area.

6) Air and substrate sniffing were frequently observed. When sniffing the air, the possums would often sit or stand on their hind legs, body upright, with forelegs held close to their body, and nose extended. On other occasions the possums appeared to be sniffing the air (head up), or substrate (head almost touching substrate), with all four feet on the ground. They did this as they moved about the cage. At times when the possums seemed intensely interested in an odour, they appeared to touch the substrate with the filtrum of their noses while moving their heads back and forth over this area. A wet mark was usually left on the substrate following these incidents.

7) Autogrooming, unlike allogrooming which was rare and very brief (at least out of the nest box), was frequently observed, and occurred both in and out of the nest box. Washing and grooming of the face and hands usually followed feeding but could occur at any time. The possum would alternatively lick its two forefeet and claws and then repeatedly rub them forwards over the sides of its face and towards the nose. All areas of the body were groomed. Face, rump and flanks were scratched and combed with the syndactylous claws and forefeet which were then licked. These grooming behaviours were similar to those recorded in *Tarsipes rostratus* (Russell, 1986) and *T. vulpecula* (Biggins, 1984). Allogrooming was observed on a few occasions. On each occasion a particular male was involved and appeared to initiate the interaction. Only once did the recipient (a female) reciprocate.

10) When the possums were returned to their home cage after a period away (e.g., a week but *not* less than 4 days) they were always repulsed from occupied nests if they attempted to enter them immediately. Thomson and Owen (1964) reported a similar incident occurring in the field.

11) Occasionally the possums chewed bark off the branches they were sitting on. They then either ate this bark (or so it appeared),

dropped it on to the ground, or returned to the nest box with it. Consequently these areas of branch, as well as the dropped pieces of bark, would have traces of saliva on them. These areas may also carry a visual message.

DISCUSSION

The odour preference results showed that the latency to approach the urine samples was significantly longer than that for any other samples, but that males spent more time sniffing familiar female urine samples. The latter information suggests that urinary odours are not aversive. Some information about the donor may be obtained from a distance. Not only is urine an odorous eliminatory product but also the odorous secretions from the paracloacal glands are voided with the urine (Bolliger & Whitten, 1948; Biggins, 1979). A variety of factors has been shown to alter the odoriferous qualities of the eliminatory products and scent gland secretions. These include diet and physiological state, which is affected by age, sex, reproductive state, and dominance status (Biggins, 1979). Specialised exocrine glands are under hormonal control and hence may indicate an animal's hormonal state. Analysis of the paracloacal gland secretions of *T. vulpecula* showed that secretions of adult males, adult females, juveniles, and socially stressed males were all different, especially with respect to the volatile secretions (Biggins, 1979).

The male response to female urinary odours suggests that they recognise females from their own nesting group and may focus their attention on these urinary odours so that they can assess the female's reproductive state. It is likely to be the male that seeks out the female, and continuous checking would ensure that he secured a mating. Other marsupials such as macropodids (Kaufmann, 1974a,b, 1975; Croft, 1981 a,b) and dasyurids (Croft, 1982) also reportedly use urinary cues to assess the female's reproductive state.

The importance of urine and the paracloacal gland secretions in ringtail possum communication was supported by marking behaviours involving micturition, such as urine dribbling and urine squirting, which are dispersive methods of urine distribution promoting the spread of the secretions.

The male ringtail possums performed urine dribbling (or cloacal dragging) more than the females. In other species, such as *T. vulpecula* (Winter, 1977; Biggins, 1979) and *P. breviceps* the same pattern is found. In the present study females increased their level of marking when placed individually in the rabbit cages. In both sexes marking occurred when the possums were aroused, especially in response to interference by the investigator. When male and female

Sminthopsis crassicaudata are housed together only the male marks, but when separated, both sexes mark (Ewer, 1968). Female ringtail possums also used a 'latrine' for micturition when males were present. Female *Dasyuroides byrnei* are also known to defecate and micturate in specific locations of the cage rather than throughout the cage as the males do (Aslin, 1974). Therefore, although marking in the ringtail possums may have been a response to the investigator, in females it may also have been due to the lack of male odour.

Urine squirting was not sexually differentiated, and has been observed in *T. vulpecula* (Winter, 1977). In the present study the urine usually contained large quantities of paracloacal gland secretion and frequently pure secretion was also voided. This behaviour always occurred when the possums were highly aroused. Increased arousal as a causal factor for scent marking involving micturition and defecation, is in agreement with the hypothesis that scent marking has evolved from autonomic responses (Morris, 1956; Kleiman, 1966). Its function appears to be one of familiarising the animal with its environment and reassuring it in unknown situations. Therefore the paracloacal secretion may indicate fear, and as it was so pungent it may have been used to rapidly disseminate the possum's own odour, saturating the immediate environment with it, and masking any other odours, thus enhancing the possum's confidence as suggested for *T. vulpecula* (Biggins, 1979, 1984). Also, because of its pungency and because it was frequently performed when being caught, it may function to ward off predators. This has also been suggested by Thomson and Owen (1964), but has generally been disputed.

Fur samples were manipulated significantly less than any of the other samples. Due to nest sharing, the fur odours were likely to represent a group odour. Self-anointing with salivary odours by auto-grooming, followed by close contact with the other possums in the nest, would result in the transfer and mixing of these odours and hence the development of a group odour. The possums micturated and defecated in their nests. This would also result in passive marking of those sharing the nest. Fur sniffing occurs in encounters between unfamiliar *Gymnobelideus leadbeateri* and may involve detection of community specific odours (Smith, 1980). The rejection of ringtail possums on reintroduction to their home cage was immediate and may have been on the basis of the missing group odour.

However, clean filter paper was also frequently manipulated (times not recorded). Therefore, the manipulation behaviour may not have been in response to the odour itself, but a stereotyped response as a result of boredom. This same behaviour has been recorded in opossums (Glickman & Sroges, 1966). With long term confinement or inferior living areas, stereotyped behaviour which tends to block attention to environmental stimulation occurs and decreases the mag-

nitude of the animal's responses (Hediger, 1955). The behaviour referred to here, was frequently performed by the male which had been housed in the rabbit cage for an extended period, thus supporting this idea. However, this behaviour is also related to nest building which was stifled due to a lack of available nesting materials.

Although saliva and faeces did not appear to be significantly investigated in the context of the odour preference experiment, their importance may have been underestimated due to the experimental conditions. The presence of labial glands (Biggins, 1979) and nasonasal sniffing, and the exudation of paracloacal gland secretions along with the faeces indicate that these odour sources may be of communicatory significance to the ringtail possum. Further studies are required to elucidate the importance of oral secretions, and faeces in olfactory communication in this species.

The limited responses to the odour samples in the Odour Preference Experiment may have been due to the conditions under which the experiment was conducted. Jenkins (1985) found that *Aepyprymnus rufescens* would not respond to odour stimuli when placed in test cages. These cages appeared to induce high levels of anxiety. One wild female, particularly, showed signs of such extreme agitation that she could not be tested. Also, the frequent interference by the investigator changing the odour samples maintained the possums in a constant state of arousal, hence possibly inhibiting or reducing their responses.

The choice of a sniffing attraction test may also have affected the results as Johnston (1981) has found that two choice preference tests were less subject to variability. Preference tasks also provide finer distinctions and hence greater accuracy (Wellington, Beauchamp, & Smith, 1981). The discrimination method used in the present study enables two odours to be compared and may enable fine distinctions to be made. Consequently, this may be a more appropriate method for testing the salivary and faecal odours.

Five possums were successfully trained in the discrimination experiment to discriminate between urinary odours of individual ringtail possums, thus showing that they were able to discriminate between sexes and individuals using urinary cues. Therefore urine, or the paracloacal gland secretions it carries is a socially significant odour for ringtail possums.

A variety of constituents in urine may have acted as cues for discrimination purposes. As mentioned above, urine samples vary with diet, hormonal state and associated factors. The quantity of paracloacal gland secretion also varies with the individual's motivational state. These differences would enable a possum to discriminate between individuals. However, whether these possums can recognise individuals is yet to be determined.

It is evident that male and female urinary odours are significantly different from each other and that the differences are identifiable by both males and females. This was indicated in the odour preference experiment, and by the differential reactions of the males and females to the odours in the odour discrimination experiment. For example, one male became extremely excited when presented with female urine samples, and mouthed them, but immediately urine dribbled when presented with male odours. Other evidence such as male interest in female micturition sites, urine dribbles and the female cloacal region further indicate that female urine contains female specific odours. Gas chromatography traces of ringtail possum paracloacal secretions (Biggins, 1979) confirm the apparent difference in odoriferous properties between male and female secretions.

One female refused to participate when the discrimination was between two foreign male odours. She was later found to be carrying a pouch young. This suggests that females are able to distinguish between male and female odours, and emphasizes that it is essential to assess all the possible factors affecting an animal's responses.

The odour samples and even the water samples were occasionally mouthed, indicating the use of the vomeronasal organ in obtaining the relevant information. The vomeronasal organ appears to be sensitive to liquid-borne olfactory stimuli (Wysocki, Wellington, & Beauchamp, 1980) and is a receptor for odours of low volatility (Powers, Fields, & Winans, 1979). The mouthing behaviour and the fact that the possums closely sniffed the odour samples in both the odour preference and discrimination experiments indicated that the important factors were nonvolatile substances. Also, the odour samples frequently dried before the possum had made its choice, but this did not appear to alter the animal's performance, further suggesting that the essential constituents for discrimination were not volatile.

No definitive conclusion can be made as to the function of the paracloacal glands, but it is evident that these glands are used when the possums are frightened or highly aroused. Therefore it may be a submissive signal, or have an anti-predatory function. Urine may carry community specific information, and information on the identity, sex and age of an animal. Unfortunately, it is impossible to put the information in perspective without the support of a field study providing detailed information on olfactory communication. Consequently, this has been the biggest limitation in this study. However, this is the first study to have successfully used the powerful technique of operant conditioning to investigate olfactory communication in a marsupial. It has shown that the ringtail possum exhibits odour preferences and is able to discriminate between conspecific urinary odours, demonstrating that olfaction is an important mode of communication in this species.

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PRIMARY FRUSTRATION IN THE RED OPOSSUM (*LUTREOLINA CRASSICAUDATA*)

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ABSTRACT: Red opossums (*Lutreolina crassicaudata*) were trained in a Y-maze to locate a piece of food (the initial response, Ri) and afterwards to run back to the start box (the final response, Rf) where no reward was available immediately although a new trial was scheduled after a 30-s intertrial interval. Omission of food in some of the training sessions (Sessions 2, 10, 20, and 30) led to a decrement in latencies of the Rf, but only in Sessions 10 and 20, which was interpreted as evidence that primary frustration elicited by omission of an expected reward increases the vigor of ongoing instrumental behavior. The absence of this effect in the first and last extinction sessions ruled out an account based on post-ingestion factors, such as transitory satiation. The results are discussed in relation to vertebrate research on learning phenomena thought to depend on the frustrative consequences of nonreward.

Didelphid marsupials reject a low concentration sugar solution significantly more if they have been preexposed to a high concentration solution in that environment, a phenomenon named successive negative contrast (SNC; Papini, Mustaca, & Bitterman, 1988). This effect has long been known to occur in other mammalian species which are shifted from a high to a low magnitude of reward or from a preferred to a less preferred food item (Cowles & Nissen, 1937; Crespi, 1942; Elliott, 1928; Flaherty, Becker, & Cheeke, 1983; Tincklepaugh, 1928).

The explanation of SNC offered by frustration theory (Amsel, 1958, 1962) is based on the notion that the discrepancy between the expected and the actual amount of food generates primary frustration, an aversive emotional response which disrupts the actual consumption of less preferred food. Frustration is also conditioned to the apparatus cues so that in subsequent trials both approach and consumption can be disrupted by anticipatory frustration (Flaherty, 1982). Primary frustration is also assumed to energize ongoing instrumental responses, an effect first reported by Amsel and Roussel (1952). In their experiment, rats were exposed to a double-alley run-

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way in which the omission of an expected reward in the first goal box led to an increase in the speed of running in the second alley.

Although post-ingestion factors play some role (Seward, Pereboom, Butler, & Jones, 1957), they cannot account for the results of other experiments suggesting that it is the omission of an expected reward that energizes behavior, whether this is produced by summation of frustration and hunger (Amsel, 1958, 1962; Spence, 1960) or by escape from frustration (Daly & Daly, 1982). The effect, for instance, does not appear in a group never rewarded in the first goal box (Wagner, 1959), and is directly related to the number of rewarded trials before omission (Hug, 1970a; Stimmel & Adams, 1969; Yelen, 1969), and to the amount of reinforcement in the first goal box in a within-subject experiment (Peckham & Amsel, 1967). Particularly important are experiments showing that the magnitude of the frustration effect changes during training, a result difficult to account for by post-ingestion factors such as temporary satiation which should permanently affect performance (Amsel & Ward, 1965; Hug, 1970b). In Hug's experiment, for instance, reinforced and nonreinforced trials alternated in the first alley and the frustration effect in the second alley increased and later disappeared as alternation patterning developed in the first alley.

In the course of experiments on the acquisition of behavioral sequences in marsupials (Papini, Hermitte, Mustaca, & Haut, 1989), we gathered information on primary frustration in red opossums. Animals were trained in a Y-maze task to run in each trial to one of the arms where food was accessible and, after its consumption, to run back to the start box where food was never available. Trials were separated by a fixed intertrial interval. In this situation, unlike the double runway experiments, only one reinforcer was delivered per trial, although two responses were required to collect it: running from the start box to the baited arm (the initial response, R_i) and running back to the start box (the final response, R_f) after consumption of the food. Interspersed among training sessions were four extinction sessions in which no food was available in the previously baited arm. The main questions were whether the R_f latencies would decrease below the level observed in trials with reward available, and whether this would occur only after some training but not initially, a pattern necessary to discard post-ingestion factors in this situation.

METHOD

Animals

Four, 42-week old red opossums, three males and one female, with free-food weight between 360 g and 600 g, served as subjects.

The animals were from the same litter, born in the laboratory. They were deprived to 80% of their ad lib weight. Each animal was housed individually with water continuously available. These animals had received prior training in this task under the same conditions used in the rewarded sessions of the present experiment. That training ended 15 weeks before the start of the present experiment and the results were reported separately (Papini et al., 1989). During the interval between experiments animals had free access to water and food (Ladrina^(R) dog chow supplemented with eggs and vitamins).

Apparatus

Training was carried out in a Y-maze with a start box separated from the rest by a guillotine door. The maze was built with wood, fully lined with plastic, and covered by transparent lids with the exception of the start box which had a wooden lid. The walls of the start box were black, whereas the rest of the maze had white walls. The floor of the maze was light blue. At the end of each arm there was a container with food which was accessible only in the correct arm. The maze was illuminated by three lamps (7 W) placed above each food container and in the start box, 15 cm from the floor. The maze was 60 cm high, 40 cm wide, 95 cm long in the central alley, 79 cm long in each arm, and 40 cm long in the start box. It was located in a sound-attenuated room where temperature varied between 20° and 27° C.

Procedure

Animals received 10 trials per day during 30 daily sessions in a spatial discrimination task. In each session, the subject was brought to the maze room in its cage and gently transferred to the start box where it remained for 30 s. The guillotine door was raised after that interval and at the same time a digital timer was manually started. The introduction of the animal's nose into the container was the criterion to stop the timer which was counting the Ri latency. Each trial was rewarded with a 2 g ball of crude meat. The food was eaten immediately and subsequently the animal usually licked the container and left the place, the whole sequence lasting 10-20 s. The final time the animal moved its nose away from the food container was the criterion to initiate a second timer which recorded the Rf latency, or the time required to go from the food container back to the start box. Once the animal entered the start box, the guillotine door was lowered and the Rf timer was stopped. A new trial started after an inter-trial interval of 30 s. After the last trial, the animal was kept in the start box for 30 s and then gently placed back in its cage and carried to the colony room, where 30 min later received access to food for 45

min (this was enough to maintain deprivation level constant during training). Water was continuously available in the cage.

Sessions 2, 10, 20, and 30 were extinction sessions. The initial 2 trials of these sessions were rewarded but reward was withheld during the last 8 trials of the session. The inaccessible food placed in the wrong arm was also withdrawn.

RESULTS

Despite prior training in this situation, latencies (transformed to the \log_{10} for the purpose of statistical analyses) were relatively high initially in training, and gradually decreased during training. A test on the first two trials of each session, which were always rewarded, indicated a significant latency decrement for both Ri ($F(29,87) = 2.35$, $p < .025$) and Rf ($F(29,87) = 3.82$, $p < .001$).

The effect of extinction was analyzed by comparing the latencies obtained in trials 3-10 of the four extinction sessions (2, 10, 20, and 30) with those obtained in the corresponding trials of the immediately preceding session. The Ri latencies were slightly increased by extinction but not enough to yield a significant difference between the comparable pre-extinction and the extinction sessions. There was a tendency toward the end of the extinction sessions for subjects to run more slowly from the start box to the previously baited arm, reflected in a significant Session by Trial interaction for the first, second, and third tests ($F_s(7,21) > 2.60$, $ps < .05$); the effect disappeared in the last extinction session.

The results for the Rf latencies are depicted in Figure 1 for each of the test sessions separately. Here extinction produced the opposite effect: it decreased the Rf latencies below those obtained in the pre-extinction session, although the size of the effect varied across tests. The statistical analyses showed that latencies did not differ during the first extinction session (none of the factors reached a significant level); the lower latencies in Session 2 than in Session 1 were caused by one animal which ran consistently faster than in the first session. Latencies during extinction were significantly decreased in Session 10 ($F(1,3) = 151.62$, $p < .005$) and Session 20 ($F(1,3) = 19.48$, $p < .025$). The last extinction test (Session 30) yielded non-significant differences, which may be a consequence either of a floor effect (i.e., an efficient performance of the Rf in the pre-extinction session), or of higher latencies in the extinction session (i.e., anticipation of extinction may have diminished the frustrative effects of reward omission). Simple analyses of the pre-extinction (Sessions 19 vs. 29) and extinction (Sessions 20 vs. 30) sessions failed to detect any significant difference.

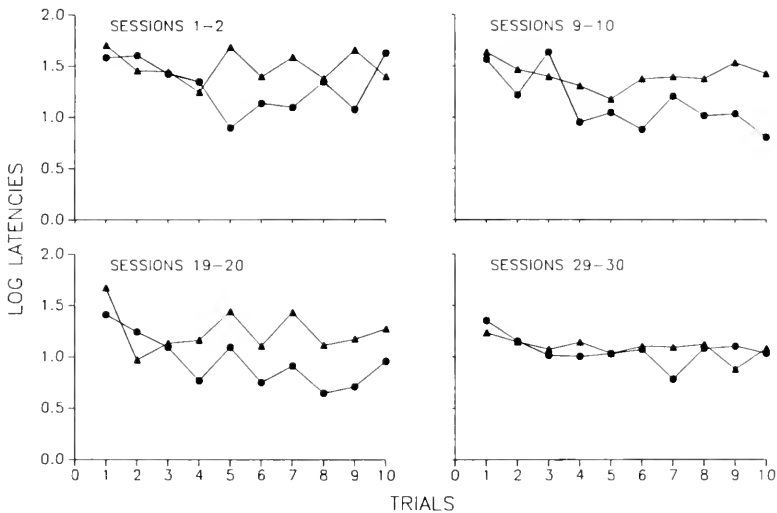


FIGURE 1. Final response (Rf) latencies during pre-extinction (triangles) and extinction (circles) sessions. There were four extinction sessions (2, 10, 20, and 30). Trials 1 and 2 were rewarded in all cases.

DISCUSSION

Omission of food decreased the latency to return to the start box only in Sessions 10 and 20 but not in Session 2. The effect was also absent in Session 30 but the reason for this seems different. The absence of the effect in Session 2—which contradicts an account based, for instance, on temporary satiation—can be interpreted in terms of frustration theory as produced by an incomplete acquisition which attenuated the otherwise frustrative effects of reward omission. On the other hand, the absence of the effect in Session 30 may reflect either a floor effect produced by low latencies during the pre-test session, or the absence of the energizing effect of reward omission during the test session.

A clear frustration effect emerged in Sessions 10 and 20, when latencies during the pre-test sessions were not yet asymptotic. The effect was relatively strong, appearing after a single exposure to reward omission, and remaining strong for the rest of the session. Particularly interesting is the fact that extinction caused not only a decrement in Rf latencies but also an increment in Ri latencies toward the end of the session. This pattern suggests that, whereas the omission of food facilitated subsequent responding, (i.e., Rf), it extinguished antecedent responses (i.e., Ri). Evidence that reinforcement

plays both a retroactive and a proactive role in the acquisition of this response sequence was also found in rats (Papini & Silingardi, 1989).

The present results are analogous to what others found in rats (see Introduction) and complement a previous experiment in which evidence of SNC was found in these marsupials (Papini et al., 1988). Together they suggest that primary and anticipatory frustration controls instrumental behavior in didelphid marsupials in the same way that it does in rats. It remains to be determined whether frustration can be counterconditioned in marsupials, a mechanism assumed to underlie the partial reinforcement extinction effect in rats (Amsel, 1958, 1962). This communality in learning processes between rats and opossums is important because some of the effects thought to reflect the operation of frustration mechanisms, such as the SNC and the partial reinforcement extinction effect, have failed to appear in teleost fish (Couvillon & Bitterman, 1985; Gonzalez, Potts, Pitcoff & Bitterman, 1972; Longo & Bitterman, 1960; Lowes & Bitterman, 1967; Mackintosh, 1971; Schutz & Bitterman, 1969), toads (*Bufo arenarum*, Schmajuk, Segura, & Ruidiaz, 1981), and turtles (*Chrysemys picta*, Pert & Bitterman, 1970; Pert & Gonzalez, 1974). Further comparative studies should show the extent to which frustration theory applies to the instrumental learning of species other than mammals and birds (Roberts, Bullock, & Bitterman, 1963).

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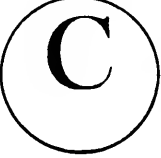
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